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# THE LIFE HISTORIES OF TWO CADDISFLY SPECIES AND THEIR MICRO-DISTRIBUTIONS WITH RELATION TO PERIPHYTON

by

(C) GAEL OGILVIE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL 1986

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.....

Supervisor

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.....

Date 10 June 1980

**Abstract**

I investigated the life histories and micro-distributions of two caddisflies, *Oligophlebodes zelti* (Limnephilidae) and *Neothremma alicia* (Uenoidae) in Dead Horse Creek, Alberta. The *O. zelti* population had a 1 year life cycle. Eggs were oviposited in July and hatched in about 20 days. Larvae grew rapidly during the remainder of the ice-free season. The larvae overwintered (November-May) in the fourth instar and molted to the fifth instar the following spring. Pupation occurred in June and adults started to emerge in mid July. The *N. alicia* population had a 2 year life cycle. Eggs hatched after freeze-up and larvae overwintered in the second instar. Most of the population was in the third instar by the following July and the fourth instar by August. These larvae spent their second winter in either the fourth or fifth instar. Pupae were observed the following July and adults began to emerge in late July. Annual production for the *O. zelti* and *N. alicia* populations was 116 $mg/m^2/yr$ and 103 $mg/m^2/yr$ respectively.

Both *O. zelti* and *N. alicia* larvae fed mainly on the fine particulate organic matter (FPOM) and diatom components of periphyton. Guts of all *O. zelti* larvae in instars two through five had between 50-65% FPOM and 23-33% diatoms. *Neothremma* larvae also fed mainly on FPOM, but larvae of the second and fifth instar consumed much more FPOM (up to 82%) than third and fourth instar larvae. These results plus scanning electron micrographs of *N. alicia* and *O. zelti* larval mouth parts indicate both species are generalist (non-selective) grazers on the periphyton.

Both *O. zelti* and *N. alicia* larvae were only found on rocks in riffles, but the two populations did not inhabit the same riffles. Riffles inhabited by *O. zelti* larvae were wider with lower slopes and water velocities than riffles dominated by *N. alicia* larvae. Average periphyton densities were greater on rock surfaces in the riffles dominated by *O. zelti*. Densities of *O. zelti* larvae and periphyton on rocks were positively correlated, but *N. alicia* larval densities were not correlated with periphyton. When periphyton densities were manipulated between rocks, more *O. zelti* larvae occurred on rocks with natural levels of

periphyton than on rocks with lower periphyton densities (bare and depleted treatments). In contrast, about equal numbers of *Neothremma* larvae occurred on rocks with bare, depleted, and natural levels of periphyton. But when periphyton densities were manipulated on individual tile surfaces, *Neothremma* larvae occurred only on periphyton patches and not on bare areas. These results demonstrate the importance of spatial scales (e.g. between riffles, between rocks, within rocks) in determining whether patchily distributed periphyton densities influence the micro-distributions of grazers in streams.

**Acknowledgements**

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Finally, I must acknowledge the populations of caddis larvae in Dead Horse Creek, Alberta that provided the conditions for discovery essential to this study.

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# I. GENERAL INTRODUCTION

Descriptive life history information is essential to most freshwater ecological studies. Interactions between an animal and its environment often change throughout its life cycle and knowledge of life histories is needed to interpret organism-environment relationships. Many aspects of freshwater benthic community structure can only be investigated with the knowledge of life histories for species within the community. For example, Anderson and Bourne (1974) showed temporal-partitioning of food resources between three co-existing Glossosomatidae (Trichoptera) species by describing the life history of each species. Life history information for aquatic insects is also needed by systematists to develop classification systems based on larval and adult stages of insects' life cycles. Wiggins (1981) outlined the importance of information on the larval stages for future classification schemes and to elucidate phylogenetic relationships within the Trichoptera.

The second chapter describes the life history of two species of Trichoptera *Oligophlebodes zelti* (Nimmo) and *Neothremma alicia* (Banks) in Dead Horse Creek, Alberta. This includes the life cycles (phenology), growth, production and also diets of each species. Before my study, the only information that was recorded for *O. zelti* was the initial species description and records of adult flight seasons in Alberta (Nimmo 1971). Swegman and Ferrington (1984) also collected *O. zelti* adults from northwestern Wyoming. *Neothremma alicia* was first described in 1930 and is widespread throughout western montane North America (Wiggins 1977). Despite this widespread distribution, the life history of *N. alicia* has not been previously reported. *Neothremma alicia* is an interesting species because Wiggins *et al.*(1985) recently reassigned the genus *Neothremma* to the Family Uenoidae that previously comprised only the type genus *Uenoa* from Asia. This decision was based mainly on larval characteristics, especially, the extremely slender body and case common to larvae of both *Uenoa* and *Neothremma*.

I was interested in the micro-distribution of *N. alicia* and *O. zelti* larvae with relation to their food source. Both species are grazers and feed by scraping periphyton from rock

surfaces (Cummins 1973). Periphyton is the complex community of algae, bacteria, fungi, protozoans, inorganic and organic detritus that is attached to the rock surface (Wetzel 1983). All growth occurs in the larval stage of Trichoptera life cycles hence it is likely that food influences larval distributions. Also, Hart and Resh (1980) found that grazing caddis larvae spend greater than 90% of their time feeding on periphyton.

Wiggins and Mackay (1978) suggested grazing caddis larvae are more common in western North America because periphyton producton is higher. Similarly Vannote *et al.* (1980) argued that more grazers occur in the downstream open (hence more productive) stretches of streams. Only a few experimental studies have been done to investigate the premise that distributions of grazers and periphyton are closely related in streams. Lamberti and Resh (1983) showed that *Helicopsyche borealis* (Trichoptera: Helicopsychidae) preferentially colonize rocks with more periphyton. Hart (1981) and Kohler (1984) found that grazers spend more time on patches of periphyton than on bare areas of tiles.

The position of a grazer in a stream must be the result of many interacting environmental variables at different spatial scales. For example, a caddis larva may be in a riffle because water velocities are higher there (as opposed to a pool), be on a rock because periphyton densities are greater on that rock, and at a position on that rock because there are other larvae at adjacent positions. To assess the extent periphyton influences the distribution of *N. alicia* and *O. zelti* larvae in Dead Horse Creek, I investigated the association between larvae and periphyton distributions on three spatial scales. I determined the distribution of both species within the study area by conducting regular surveys, then quantified periphyton densities in riffles dominated by *O. zelti* and riffles dominated by *N. alicia* larvae. Within a riffle, I expected periphyton densities on rocks to influence distributions of the larvae, because of it being energetically costly for larvae to move between rocks. I investigated whether distributions of larvae and periphyton were related on rocks in Dead Horse Creek using two approaches. First, I correlated densities of larvae and periphyton on individual rocks, and, second, I experimentally manipulated periphyton densities then quantified the

response of larvae. Because *Epeorus* sp. (Ephemeroptera: Heptageneiidae) nymphs were common in the riffles used for these experiments I also quantified the distributions of *Epeorus* sp. on treatment rocks. Finally I manipulated periphyton densities on tile surfaces to investigated whether periphyton densities influence *N. alicia* larvae distribution at this spatial scale. This type of study, incorporating life history information and using different spatial scales of investigation, will help to determine the extent to which periphyton influences distributions of grazers in streams.

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# II. THE LIFE HISTORIES AND MICRO-DISTRIBUTION OF OLIGOPHLEBODES ZELTI (TRICHOPTERA: LIMNEPHILIDAE) AND NEOTHREMMA ALICIA (TRICHOPTERA: UENOIDAE) IN DEAD HORSE CREEK, ALBERTA

[1]

## INTRODUCTION

There is an urgent need to accumulate basic life history information for species of Trichoptera. In the past, taxonomic classifications have been based on the adult stages of the insects' life cycles. Today, information on the larval stages is considered essential before systematic relationships can be assessed (Wiggins 1981). The life history of any species includes its growth, production and diet. These data are needed to study energy flow within a system and hence to design fisheries management programmes (Waters 1969). It is also useful for interpreting distribution patterns of the species. With prior knowledge of species-specific life histories and distributions, experiments can be designed that require fewer samples to minimize sampling variabilities (Resh 1979).

The caddisflies *Neothremma* (Uenoidae) and *Oligophlebodes* (Limnephilidae) occur within the montane regions of Western North America (Wiggins 1977). Seven species of *Oligophlebodes* are known, but the only life cycle reported is that for *Oligophlebodes sigma* in Utah (Pearson and Kramer 1972). *Oligophlebodes zelti* (Nimmo) was thought to occur only in Alberta until a population was found in the mountains of northwestern Wyoming (Swegman and Ferrington 1984). *Neothremma* has been assigned recently to the family Uenoidae, previously comprising only the type genus *Uenoa* from Asia (Wiggins *et al.* 1985) *Neothremma alicia*(Banks) is one of six species known for this genus. The life history of *N. alicia* has not been previously reported upon, but adult flight records are known throughout its range which extends from Alberta and British Columbia to Oregon, Utah and Colorado.

---

[1]A version of this chapter has been accepted by the Canadian Journal of Zoology for publication.

I examined the life histories of *O. zelti* and *N. alicia* in Dead Horse Creek, Alberta. Phenologies, growth rates, diets, densities and annual productions are reported. Also, the morphology of the larval mouthparts are described from scanning electron micrographs. Both species graze on periphyton of riffle areas. Periphyton is defined as the complex community of algae, bacteria, fungi, protozoa, inorganic and organic detritus that is attached to the substrate (Wetzel 1983). The micro-distributions of *O. zelti* and *N. alicia* were investigated in relation to total periphyton, living algae, and other grazers on individual rocks. Distribution patterns were analysed at two levels: within the study area of the stream and within riffle sections.

## STUDY AREA

The study was conducted in the riffle areas of the last 800 m stretch of Dead Horse Creek, a first order stream located on the eastern slopes of the Canadian Rockies (50° 37' N, 114° 39.2' W) (Fig. II-1). Dead Horse Creek arises from a series of springs at an altitude of 1525 m and flows into Gorge Creek immediately below the study area at an altitude of 1452 m. The stream drains an area measuring 2.02 km$^2$. Average monthly discharge ranges from 0.0026 m$^3$/sec during August to 0.019 m$^3$/sec during spring run-off in early May. There are no temporary or permanent fish populations in Dead Horse Creek.

The average width of riffles is 1.1 m (SD=0.4 N=37) and their average water depth is 5.9 cm (SD=2.1 cm N=37). The mean slope for riffles within the study area is 5.5 % (SD=2.6 % N=28). Riffle sections comprise 77.8 % of the study area. Most riffles are shaded by white spruce (*Picea glauca*), aspen (*Populus tremuloides*) and willow (*Salix sp.*). Water temperatures, recorded with a Ryan 30-day thermograph, ranged from 0°C in the winter to 11°C in Summer (Fig. II-2). The study area was covered with thick ice from October to late May. A shallow stream of water flowed beneath the ice. In heavily shaded regions there was ice-cover until mid-June.

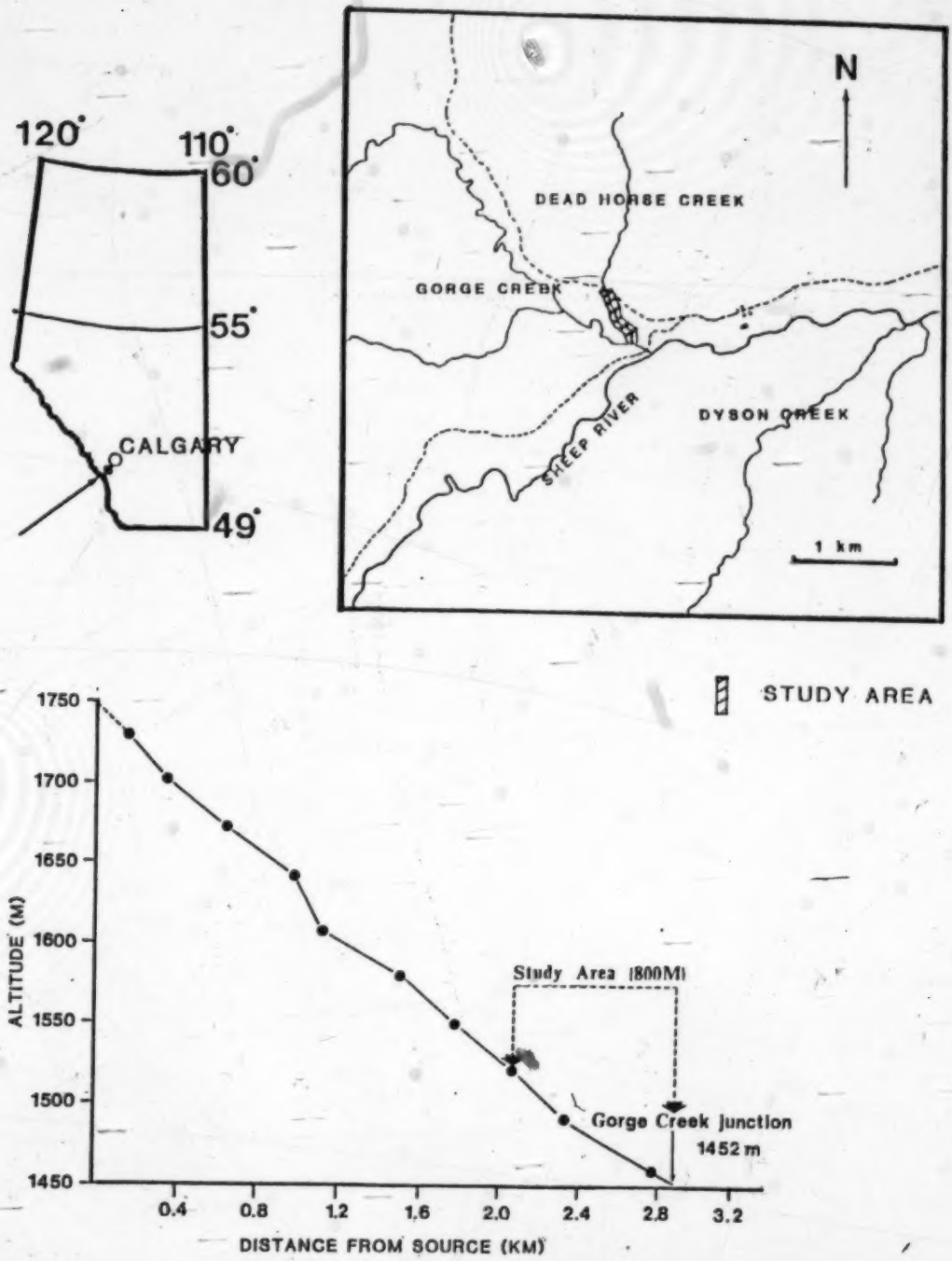


Figure II-1. Dead Horse Creek; location in Sheep River Wildlife Sanctuary (approximately 85 km S.W. of Calgary, Alberta) and altitude profile.

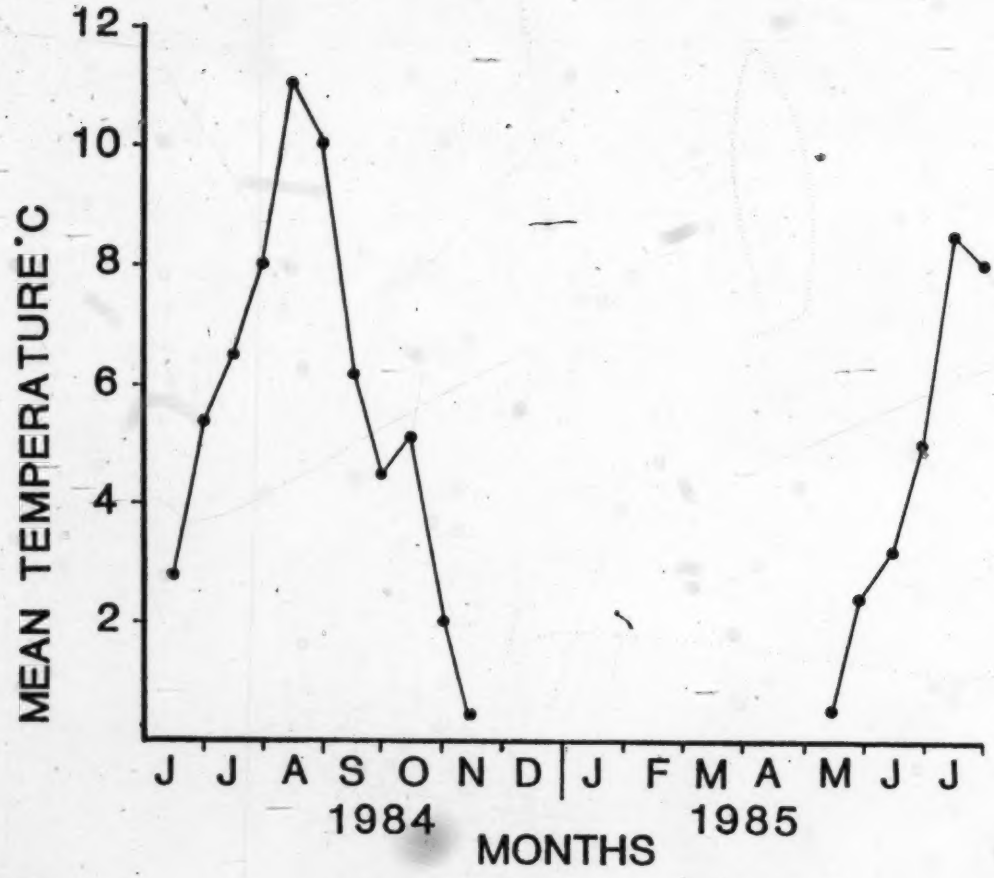


Figure II-2. Mean water temperatures within the study area, Dead Horse Creek. (Range of standard error: 0.13-0.76 °C).

# METHODS

## Life cycles

Qualitative benthic samples were collected from May 1984 to August 1985. Samples were taken once per week between May and September and four times between October and April. All samples were taken from rock surfaces within fast flowing (mean water velocity = 34 cm/sec) riffle areas. *Oligophlebodes zelti* and *N. alicia* larvae were removed with forceps, preserved immediately and counted in the laboratory under a dissecting microscope. The headwidth (distance when viewed dorsally) of each larva was measured using an ocular micrometer eyepeice at 40X magnification. Larval instars were determined by constructing frequency histograms of the headwidth data. Four jar-emergence traps were kept in the stream from July - September 1984 and from July - August 1985 to collect emerging *O. zelti* and *N. alicia* adults. The traps consisted of a wooden frame and a fine-mesh tent shaped net. An inverted jar at the apex of the net trapped the adult insects. The jars were emptied daily and the adults were preserved immediately. Small populations of *O. zelti* and *N. alicia* larvae were kept in a controlled laboratory during the winter. Water temperature was held constant at 0.5°C and daylength was adjusted every week to imitate natural field conditions. Once per month, 10 laboratory larvae were removed and their headwidths measured. In February, headwidths of laboratory larvae were compared with headwidths of larvae collected from the field.

## Production

Annual production was estimated for each species from growth rates, mean standing crops and larval densities (/m$^2$ stream bed) using the instantaneous growth method (Waters 1977). Every 2 weeks a sample of *O. zelti* and *N. alicia* larvae was collected and used to determine growth rates. Larvae were removed from the rock surfaces with forceps. Their headwidths were measured before they were removed from their cases and oven-dried at 60°C

for 72 hours. Individual larvae were weighed within 2 weeks to the nearest 0.01 mg on a Cahn gram electrobalance. Mean dry weights were calculated for each instar. Growth rates and mean standing crops were calculated using mean dry weights and proportions of each instar occurring over intervals ranging from 2 weeks to 4 months (winter data).

Two conversion factors were used to convert *O. zelti* and *N. alicia* densities per $cm^2$ of rock surface area (distribution data) to densities per $m^2$ of stream bed. The first was the ratio of surface areas supporting *O. zelti* or *N. alicia* larvae populations to the total surface area of the riffle. The top and sides surface area of all rocks with *O. zelti* or *N. alicia* larvae within a $m^2$ quadrat were measured for five randomly placed quadrats in six different riffle areas. The second conversion factor was the ratio of riffle surface area to total stream bed surface area. Widths and lengths of riffles, pools and waterfalls within the study area were measured with a meter stick. The densities of *O. zelti* and *N. alicia* larvae per $m^2$ of stream bed were calculated by multiplying densities per $cm^2$ of rock surface by these two conversion factors.

**Feeding**

To investigate *O. zelti* and *N. alicia* diets, I quantified their gut contents following the procedure outlined by Cummins (1973). Both preserved and living larvae were used. The digestive tract was dissected on a depression slide and the gut contents were teased out using a fine probe. Gut contents from one to ten larvae (depending on size and fullness of the gut) were mixed well in a small petri-dish. The sample was poured into a Millipore filter column and filtered at low vacuum (<5 PSI) onto a 0.45 $\mu$m membrane filter using a portable hand pump. The filter was placed on one to three drops of light emersion oil in a petri dish and allowed to clear at room temperature for 48 hours. This material was then mounted using Permount. Gut contents from 102 *O. zelti* and 45 *N. alicia* larvae were prepared following this procedure.

Analyses involved using a Whipple grid fitted into the eyepeice of a compound microscope. Under 400X magnification, the number of grids covered per field of view were counted for three food types: diatoms, filamentous algae and fine particulate organic matter (FPOM). Twenty five fields of view (1.8 percent of the total filter surface area) were quantified for each slide. Gut composition (%) was calculated by dividing the number of grids covered for each food type by the total number of grids covered.

To check for differences between gut passage times of the food types, individual *O. zelti* larvae were starved for varying lengths of time. Sixty fifth-instar *O. zelti* larvae were placed in separate petri dishes containing filtered stream water. Starvation time intervals were 1 hr, 2 hr, 4 hr, 7 hr, 11 hr, 25 hr, 45 hr and 65 hr. After each interval, six larvae were randomly selected, removed and immediately dissected. Slides of their gut contents were prepared and analysed using the procedure outlined above. Throughout the experiment, any inactive larvae were removed and discarded. The filtered stream water in each petri dish was changed every five hours to prevent accumulation of faeces. Slides were also made of the faecal material.

**Micro-distribution**

From May to August 1985, a quantitative survey was done every 2 weeks to investigate distributions of *N. alicia* and *O. zelti* larvae within the study area. Numbers of all macroinvertebrates on 10 rocks from 33 different riffle areas were recorded. The slope of each riffle was measured at the beginning of the first survey. Six of the riffles were selected for further study: three from the mid-section of the study area (350 to 610 m upstream from Gorge Creek junction), which were dominated by *O. zelti* larvae and three from the upstream section of the study area (610 to 800 m upstream from the Gorge Creek junction), which were dominated by *N. alicia* larvae. Water velocites along five transects, water temperatures and depths and riffle widths were measured.

Ash free dry weight (AFDW) analyses, to measure periphyton and chlorophyll *a* analyses to measure living algae were done for scrapings from 10 rocks from each of the six riffles. Periphyton from the tops and side of each rock was scraped off thoroughly using a sharp scalpel and rinsed into a flask containing filtered river water. The sample was shaken vigorously, and if the periphyton was not well mixed, it was homogenized in a Waring single speed blender for 60 seconds. The volume of the sample was measured using a graduated cylinder. Two 10 ml subsamples were taken from each periphyton sample: one for chlorophyll *a* analysis and one for AFDW analysis. Each subsample consisted of five separate 2 ml aliquots that were extracted from the middle of the flask using a volumetric pipette. The sample was shaken between each 2 ml extraction to ensure the periphyton remained well mixed. Each subsample was filtered onto a 2.4 cm glass fibre filter (Whatman GF/C) using a Millipore filter apparatus and Nalge hand vacuum pump. The filters were placed in airtight sealable petri dishes and frozen. Before freezing, magnesium carbonate was sprinkled onto the filters destined for chlorophyll *a* analysis to prevent acidification of the algae. The amount of chlorophyll *a* present was determined within 4 weeks using the acetone extraction method (Moss 1967a, b). Each filter was homogenised in 90% acetone for 60 seconds with a Polytrol sonicator. Samples were stored in the dark at 4°C for 24 hours. A Pye Unicam (350/550) spectrophotometer was used to measure absorbance of the resulting chlorophyll *a* extract. Pheophyton pigments were also measured following acidification of the extract ( Osmund Holmes-Hansen 1978).

The other subsample was dried at 60°C for 24 hours, cooled in a desiccator and weighed to the nearest 0.01 mg using a Cahn gram electrobalance. This subsample was then placed in a muffle furnace for 4 hours at 550°C, cooled and reweighed. The difference between the "ashed" and dried weights is equal to the biomass of periphyton in each subsample because all organic matter is combusted over 4 hours at 550°C (Wetzel and Likens 1979).

The surface area of the top and sides of each rock was measured by carefully wrapping them in aluminium foil. When all pieces of the foil were in direct contact with the rock they were removed and pressed flat. Surface area of the foil was measured using a Pico polar compensating planimeter. I checked the accuracy of this tecnique by replicate (3) wrappings of 10 rocks. The mean Coefficient of Variation for the 3 replicates of each rock's surface area was only 2.3% (N=10, SD=1.2%). Density of algae ($\mu$g chlorophyll *a*/cm$^2$) and periphyton (mg AFDW/cm$^2$) were calculated using the ratio of subsample to periphyton sample volume and the rock surface area.

In 1984, five rocks from 17 different riffles were sampled to investigate the distribution of *O. zelti* and *N. alicia* larvae within riffles. A total of 125 rocks were sampled between mid July and the end of October. An additional 40 rocks from 4 riffles were sampled in 1985 between mid May and mid June. Each rock was selected at random from high water velocity areas of a riffle. Water depth above the rock was recorded before it was angled slowly up towards the current and lifted from the stream bed. This removal method ensured no animals were lost downstream. In 1985 the water velocity immediately upstream was measured using a Ott C-1 current meter. All macroinvertebrates were removed from the rock with forceps. They were preserved, then counted and identified in the lab under a dissecting microscope. Headwidth measurements were taken from *O. zelti* and *N. alicia* larvae to supplement the qualitative life cycle data. Gut analyses were done on representatives of all other macroinvertebrate taxa to determine other taxa grazing on periphyton. Densities of living algae and periphyton were determined for each rock using the procedure previously outlined.

# RESULTS

## Life cycles

### *Oligophlebodes zelti*

*Oligophlebodes zelti* had a one year life cycle in Dead Horse Creek, Alberta. Eggs were oviposited on the under surface of rocks in fast-flowing riffle areas during the first weeks of August 1984 and from mid to late July 1985. The size of egg masses ranged from 0.8 - 1.2 cm in diameter. They contained an average of 111 (N=7) cream-coloured eggs enclosed in a gelatinous substance. The egg masses were always found in pairs, which may indicate each female oviposited two egg masses. In both years, oviposition occurred when densities of the flatworm *Polycelis* sp. were very high. Predation by *Polycelis* sp. on the conspicuous stationary egg masses could be a major mortality factor; I often observed empty egg masses and *Polycelis* sp. on the same rock. The surviving eggs hatched into first instar larvae in late August 1984 and in early August 1985. Twenty-one days elapsed between oviposition and hatching (N=9, 1985 data).

Five larval instars were identified for the *O. zelti* population (Fig. II-3). The larvae grew rapidly through the first three instar stages. By the beginning of ice-cover in late October 1984 the population was dominated by third instar larvae (Fig. II-4). A larval molt must have occurred beneath the ice because when I sampled in winter (22 February 1985), 80% on the *O. zelti* larvae collected were in the fourth instar. These larvae were active in a shallow stream of flowing water beneath 1-2 metres of ice. The laboratory specimens also remained active in the fourth instar stage from November to April. *Oligophlebodes* larvae molted to the fifth and final instar following the beginning of ice melt in Dead Horse Creek. By June 1985, the population was entirely composed of fifth instar larvae. In contrast, the samples taken at the beginning of June in 1984 still contained many fourth instar larvae. By the first week of June 1985, densities of *O. zelti* larvae were declining, indicating the onset of pupation. In 1984, pupae were not observed

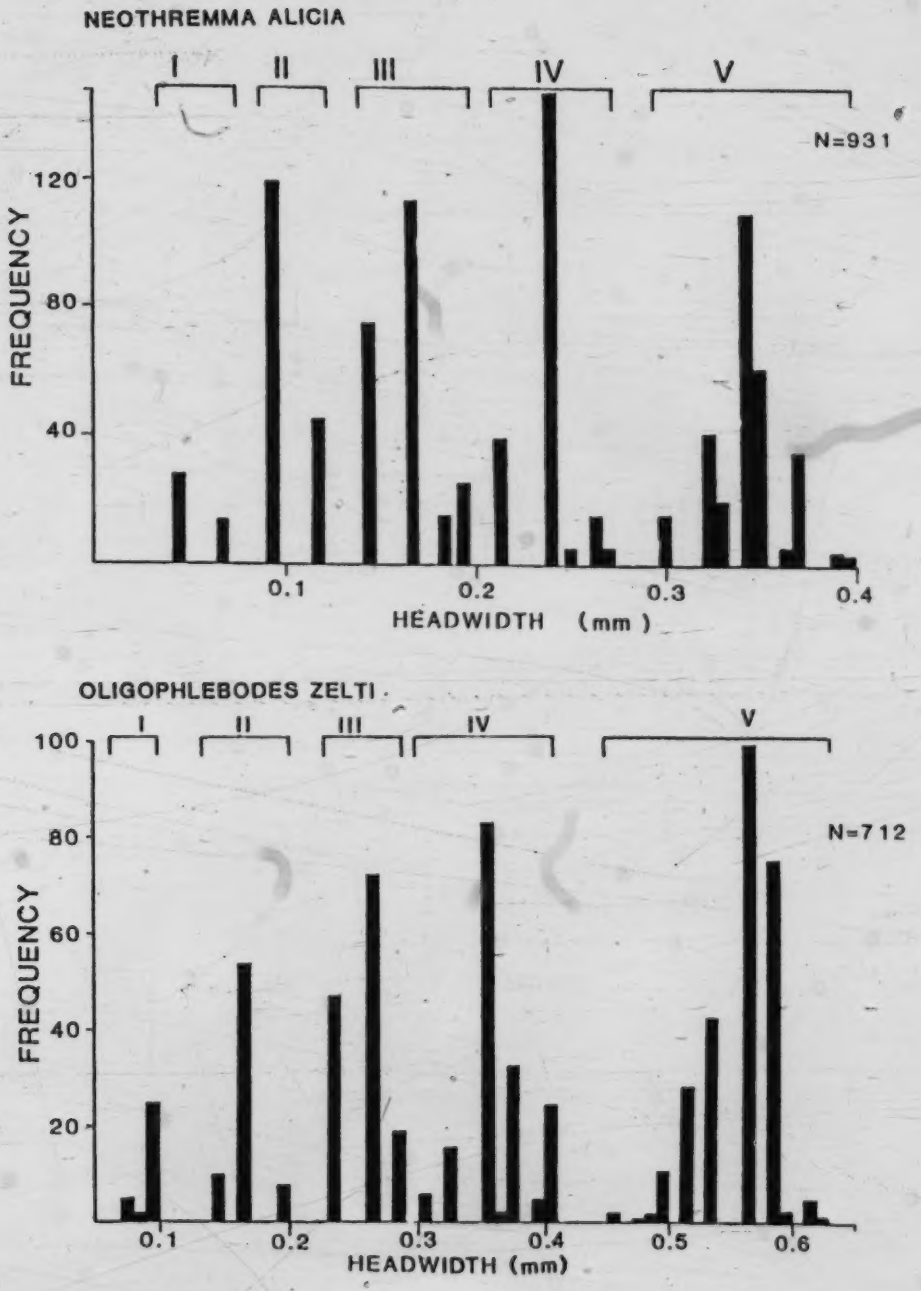


Figure II-3. Headwidth frequency histograms of *O. zelti* and *N. alicia* instars I-V. N = Total number of larval headwidths measured.

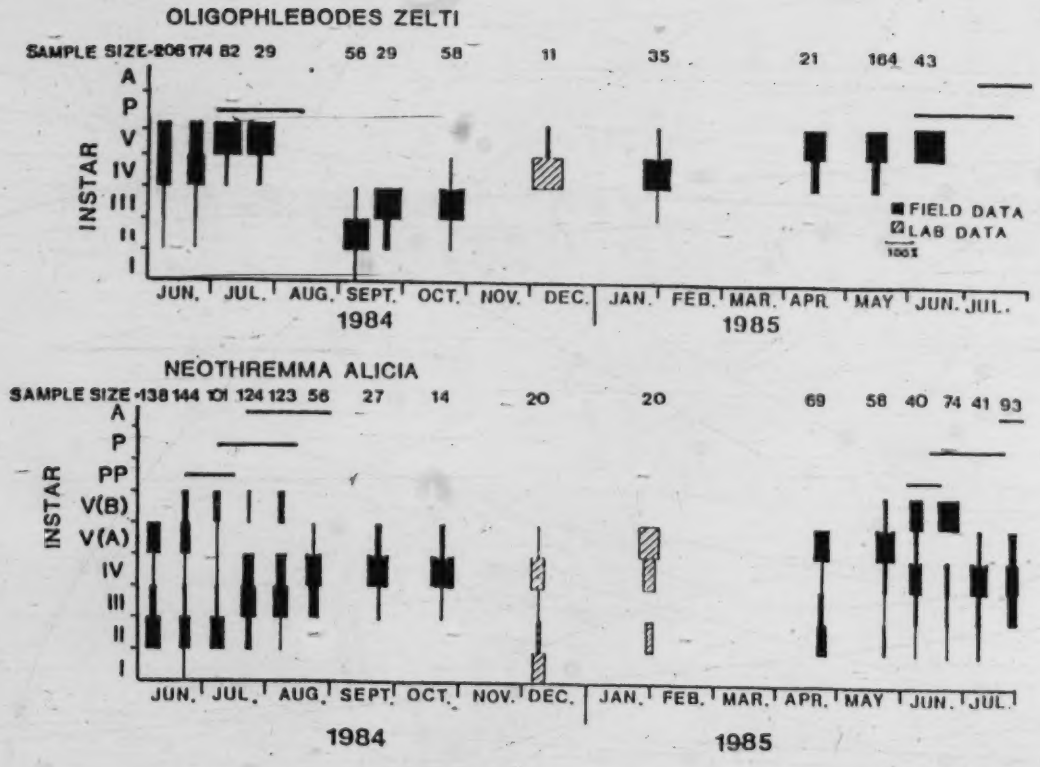


Figure II-4. Life cycle of *O. zelti* and *N. alicia* in Dead Horse Creek, Alberta from June 1984 to July 1985. The width of each bar represents the percentage of individuals in each larval stage. V(A) = *N. alicia* fifth instar larvae (mean abdomen length = 4.5 mm), V(B) = *N. alicia* fifth instar larvae (mean abdomen length = 6.5 mm). Presence of prepupae (PP), pupae (P), and adults (A) are indicated by a line.

until the final week of June.

*Oligophlebodes* pupated in rotting spruce logs that had fallen into Dead Horse Creek. They were often found deep within the log. Before pupation, the larva closed off the anterior opening of its case with a large flat pebble. The *Oligophlebodes sigma* population in Utah also used a flat pebble to seal their cases prior to pupation (Pearson and Kramer 1972). I did not observe a pre-pupal stage, and after 3 weeks the adults emerged via a hole in the pupal case. Peak emergence occurred between 16-21 July in 1985 and was not observed in 1984.

*Neothremma alicia*

The *N. alicia* population had a 2 year life cycle in Dead Horse Creek. Egg masses were very similar to *O. zelti* egg masses. The eggs could be separated from those of *O. zelti* by their different distributions within the study area. I did not observe *N. alicia* eggs hatching in the stream, but in the laboratory hatching occurred late in November, 1984.

Headwidth measures of larval *N. alicia* indicated five instars (Fig. II-3). The population spent 2 weeks in the first instar and the remainder of the winter as second instar larvae (Fig. II-4). Samples taken from the field immediately after ice-melt were dominated by second instar larvae. They remained common in the population until early July 1984. During the summer, the numbers of third and fourth instar larvae increased slowly. By the middle of October the population consisted mainly of fourth instar larvae. *Neothremma alicia* larvae spent their second winter in the fourth or fifth instar (lab population data). Fifth instars were common in the stream from immediately after snow melt until the beginning of August 1984 but only until the end of June 1985. Prior to pupation, *N. alicia* larvae increased their case length from an average of 5.4 mm to 7 mm (N=10). Abdomen length also increased from an average of 4.4 mm to 6.5 mm (N=10). I divided the fifth instar stage into two categories based on abdomen lengths : V(A) for larvae with abdomen lengths from 4.1-5.4 mm and V(B) for larvae with

abdomen lengths measuring from 5.5-7.0 mm. In 1984 V(A)instar were common until the end of June and during July fifth instar *N. alicia* larvae were all in the V(B) category.

Immediately prior to pupation the larvae attached in clusters to rock crevices and closed off their anterior case opening with a perforated silk membrane. Clusters of *N. alicia* ranged in size from 2 to 40 pupae. A pre-pupal stage that lasted 1-3 weeks was observed. Pupation took another 1-3 weeks. *N. alicia* pupae were first collected on 8 July 1984 and as early as 14 June 1985. Adults emerged by cutting a hole in the side of the pupal case. They were caught in emergence traps between 16 July and 31 August 1984.

**Production**

Mean dry weights for *N. alicia* and *O. zelti* larval instar stages are shown in Table II-1. Between September and October 1984, mean density of *O. zelti* was 170 larvae/m² (over total stream bed). Density estimates for spring 1985 were much lower indicating that some mortality occurred in the population, either during ice-cover or high water of spring. Mean density for the population in May 1985 was 83 larvae/m², following the onset of pupation densities decreased steadily. *Neothremma alicia* larvae occurred at an average density of 137/m², over the total stream bed, between June and October 1984. I did not measure *N. alicia* densities in 1985 because I was sampling quantitatively from only the mid-section of the study area. Because *N. alicia* has a two year life cycle with overlapping generation in Dead Horse Creek I was able to use the 1984 density estimate for 1984 and 1985 production calculations.

Annual production was calculated by summing the production over 12 time intervals for *O. zelti* (Table II-2) and 9 time intervals for *N. alicia* (Table II-3). I calculated mean weights for each time interval by summing the number of larvae in an instar multiplied by the instar's mean weight, for all instars, then dividing this total by the number of larvae in the

Table II-1. Mean dry weights and standard deviations (mg) for *O. zelti* and *N. alicia* larval instars. Individual larvae were dried at 60°C for 24 hr, cooled and weighed using a Cahn Electrobalance. V(A) = Instar V larvae (mean abdomen length = 4.4 mm), V(B) = Instar V larvae (mean abdomen length = 6.5 mm).

| | Sample Size | Mean weight(mg) | Standard deviation(mg) |
|---|---|---|---|
| *O. zelti* | | | |
| Instar I | 1 | 0.02 | |
| II | 10 | 0.07 | 0.03 |
| III | 19 | 0.10 | 0.08 |
| IV | 43 | 0.27 | 0.13 |
| V | 38 | 0.78 | 0.51 |
| *N. alicia* | | | |
| Instar I | 1 | 0.03 | |
| II | 9 | 0.05 | 0.04 |
| III | 34 | 0.12 | 0.06 |
| IV | 58 | 0.29 | 0.13 |
| V(A) | 37 | 0.61 | 0.24 |
| V(B) | 7 | 1.33 | 0.32 |

Table II-2. Calculation of annual production for *O. zelti* in Dead Horse Creek, Alberta using the instantaneous growth method. G=instantaneous rate of growth; Ln (Wt/W(t-1)), B=mean standing crop; (Bt + B(t-1))/2, P=production for the interval between successive dates. The line separates cohort 1(hatched 1983) and cohort 2 (hatched 1984).

| Date | Standing Crop(Bt) ($mg/m^2$) | Mean Weight(Wt) (mg) | G | B ($mg/m^2$) | P=GB ($mg/m^2$) |
|---|---|---|---|---|---|
| 28.5-10.6.84 | 38.0 | 0.45 | | | |
| | | | 0.02 | 38.3 | 0.77 |
| 11.6-24.6.84 | 38.7 | 0.46 | | | |
| | | | 0.46 | 42.8 | 19.69 |
| 25.8-8.7.84 | 47.0 | 0.73 | | | |
| | | | 0.07 | 39.0 | 2.73 |
| 9.7-23.7.84 | 31.1 | 0.78 | | | |
| 10.8-15.8.84 | 2.0 | 0.02 | | | |
| | | | 1.25 | 6.8 | 8.50 |
| 16.8-3.9.84 | 11.7 | 0.07 | | | |
| | | | 0.00 | 11.7 | 0.00 |
| 4.9-15.9.84 | 11.7 | 0.07 | | | |
| | | | 0.25 | 14.0 | 3.50 |
| 16.9-30.9.84 | 16.4 | 0.09 | | | |
| | | | 1.17 | 31.1 | 36.39 |
| 1.10-25.10.84 | 45.8 | 0.29 | | | |
| | | | 0.30 | 39.2 | 11.76 |
| 26.10.84-21.2.85 | 32.7 | 0.39 | | | |
| | | | 0.43 | 41.5 | 17.84 |
| 22.2-3.5.85 | 50.4 | 0.60 | | | |
| | | | 0.26 | 57.6 | 14.98 |
| 4.5-28.5.85 | 64.9 | 0.78 | | | |
| Mean Standing Crop = | 32.5 | | | Annual Production = | 116.16 |

Table II-3. Calculation of annual production for *N. alicia* in Dead Horse Creek, Alberta, using the instantaneous growth method. G=instantaneous rate of growth; Ln (Wt/W(t-1)), B=mean standing crop; (Bt + B(t-1))/2, P=production for the interval between successive dates. 1a-5a=cohort 1(hatched 1982), 1b-9b=cohort 2(hatched 1983) 7c-10c=cohort 3(hatched 1984). Standing crops for each interval were combined to calculate mean standing crop.

| Date | Standing Crop(Bt) ($mg/m^2$) | Mean Weight(Wt) (mg) | G | B ($mg/m^2$) | P=GB ($mg/m^3$) |
|---|---|---|---|---|---|
| 1a. 28.5-12.6.84 | 30.6 | 0.56 | | | |
| | | | 0.36 | 46.4 | 16.70 |
| 2a. 18.6-2.7.84 | 62.3 | 0.80 | | | |
| | | | 0.32 | 55.2 | 17.66 |
| 3a. 3.7-15.7.84 | 48.1 | 1.10 | | | |
| | | | 0.19 | 33.1 | 6.29 |
| 4a. 16.7-31.7.84 | 18.2 | 1.33 | | | |
| | | | 0.00 | 26.3 | 0.00 |
| 5a. 1.8-15.8.84 | 34.5 | 1.33 | | | |
| 1b. 28.5-12.6.84 | 5.8 | 0.07 | | | |
| | | | 0.00 | 4.8 | 0.00 |
| 2b. 18.6-2.7.84 | 3.8 | 0.07 | | | |
| | | | 0.25 | 6.3 | 1.57 |
| 3b. 3.7-15.7.84 | 8.8 | 0.09 | | | |
| | | | 0.57 | 14.7 | 8.38 |
| 4b. 16.7-31.7.84 | 20.6 | 0.16 | | | |
| | | | 0.12 | 20.4 | 2.45 |
| 5b. 1.8-15.8.84 | 20.3 | 0.18 | | | |
| | | | 0.20 | 23.1 | 4.62 |
| 6b. 17.8-18.9.84 | 25.9 | 0.22 | | | |
| | | | 0.24 | 28.2 | 6.77 |
| 7b. 19.9-25.10.84 | 30.5 | 0.28 | | | |
| | | | 0.68 | 36.7 | 24.96 |
| 8b. 26.10.84-17.5.85 | 42.9 | 0.55 | | | |
| | | | 0.09 | 50.1 | 4.51 |
| 9b. 18.5-28.5.85 | 57.4 | 0.60 | | | |
| 7c. 19.9-25.10.84 | 1.8 | 0.03 | | | |
| | | | 0.98 | 3.3 | 3.23 |
| 8c. 26.10.84-17.5.85 | 4.8 | 0.08 | | | |
| | | | 0.92 | 6.0 | 5.52 |
| 9c. 18.5-28.5.85 | 7.3 | 0.20 | | | |
| Mean Standing Crop= | 47.1 | | | Annual Production= | 102.66 |

entire population. Mean weight was multiplyed by larval density for that time period to give standing crop estimates. The annual production for *O. zelti* in Dead Horse Creek was 116.16 mg/m²/year and for *N. alicia* was 102.66 mg/m²/year.

Daily growth rates were calculated by dividing the difference between the mean dry weights by the number of days between the mid-points of consecutive time intervals. The average daily growth for *O. zelti* was 4.7 μg (N=9 SE=1.9 μg); the highest growth rates occurred prior to pupation (18 μg/day). The *N. alicia* population also grew rapidly prior to pupation; in June and early July larvae grew 13.3 μg/day. For the earlier *N. alicia* larval stages the average growth was only 1.8 μg (N=9 SE=0.45 μg). The annual turnover ratio or ratio of production to mean biomass (P/B) for *O. zelti* was 3.6 and for *N. alicia* was 2.2. The turnover ratio for both populations were within the general range reported for aquatic invertebrates (2-5, Waters 1969).

**Feeding**

*Oligophlebodes* and *Neothremma* larvae feed mainly upon fine particulate organic matter (FPOM) and diatoms (Fig. II-5). Guts of all *O. zelti* larval instar comprised 50-65 % FPOM and 23-33% diatoms. Gut contents of *N. alicia* instars were more variable. Guts of second and fifth instars contained mainly FPOM (82% and 68% respectively) and guts of third and fourth instar larvae contained higher percentages of diatoms. *Cocconeis, Navicula* and *Meridion* were common diatom genera found in the guts of both *O. zelti* and *N. alicia* larvae. These diatoms ranged in size from 17- 70 μm. Filamentous algae were rarely found in the guts of either species with the exception of second instar *O. zelti* larvae.

After 65 hours of starvation (laboratory conditions) there was little change in the relative pecentage composition of *O. zelti* larval gut contents (Fig. II-6).. The volume of the guts decreased throughout the experiments and were very close to completely empty after 65 hours. At this time all diatoms in the gut were apparently dead since they were devoid of any cytoplasm. Insects can rapidly digest diatom cytoplasm through puncta in the cell wall

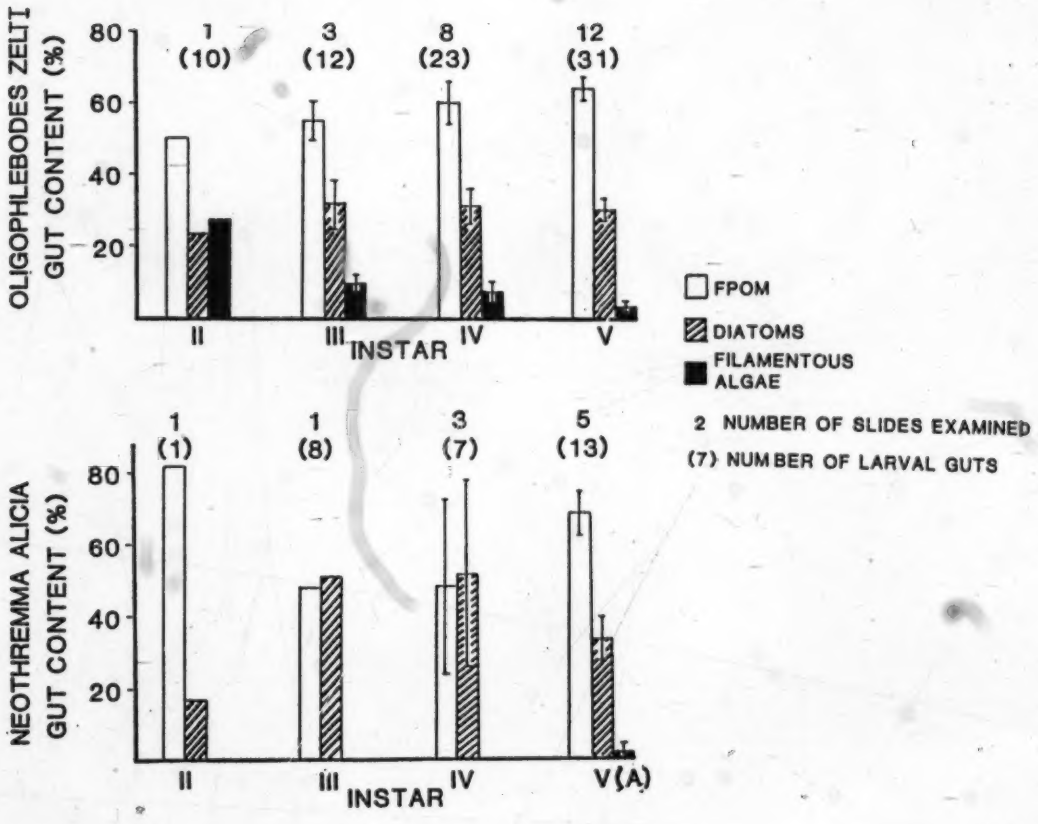


Figure II-5. Percent composition of diatoms, filamentous algae and FPOM in the gut contents of *O. zelti* and *N. alicia* larval instars II-V. Vertical lines on bars are standard errors, which were calculated using the number of slides examined for each instar. No standard error could be calculated for *O. zelti* Instar II and *N. alicia* Instars II and III because only one slide was examined for these instars.

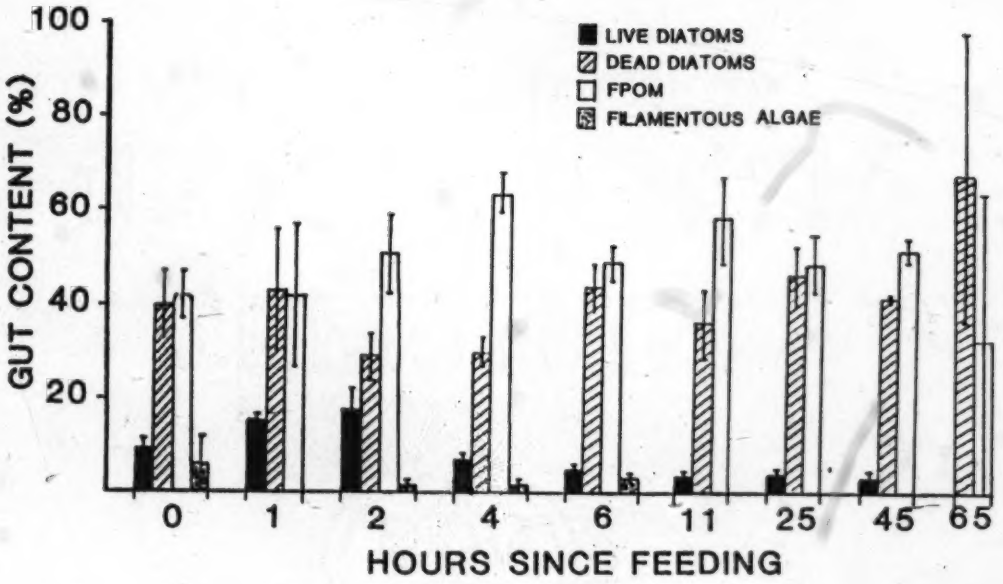


Figure II-6. Results of an experiment to determine the retention of food items in fifth instar *O. zelti* guts over 65 hours. Mean percentage composition of food types are shown for each time interval. This figure shows that percentage composition of the gut contents remained relatively constant despite the steady decrease in gut volume observed over the starvation time. Vertical lines on the bars are standard errors calculated for the number of gut content slides examined (N=3 for all periods except 45 and 65 hours when N=2).

(Lamberti and Moore 1983), and this would leave the siliceous wall within their guts. I did not distinguish between live and dead diatoms in the analysis of gut contents. If diatom cell walls are retained for longer periods of time in larval guts, their percentage composition will be over-estimated. The dominance of FPOM in *O. zelti* and *N. alicia* guts is probably a conservative estimate of FPOM contribution to larval diets.

*Neothremma* and *Oligophlebodes* larvae have scoop-shaped mandibles, which larvae use to scrape periphyton as they move across rock surfaces. The length of the outer edge of each mandible blade is approximately 75$\mu$m in both *O. zelti* and *N. alicia* fifth instar larvae (Plate II-1). Along the posterior mandible edge there is a line of stiff bristle-like setae, which could aid in the transfer of periphyton to the mouth. Maxillary and labial palps are well developed in both species and bear many setae. *Oligophlebodes* larvae have a wide labrum with two forward projecting membranous lobes. These lobes are also covered with setae which could act as a brush pushing periphyton towards the mandible. Hall and Pritchard (1975) observed the setae on *Tipula sacra* (Diptera: Tipulidae) mouthparts dislodging particles within the periphyton while the larvae were feeding. The mouth opening in *O. zelti* fifth instar larvae is 125 $\mu$m wide. (Plate II-2.)

**Micro-distribution**

In Dead Horse Creek, *N. alicia* and *O. zelti* larvae inhabit riffles, but do not occur in the same riffle (Fig. II-9). *Neothremma* larvae were found in riffles along the entire length of the stream except over a 360 m section in the middle of the study area (350 to 610 M upstream from the Gorge Creek junction). *Oligophlebodes* larvae were found only in this section. Significant differences existed for several parameters amoung riffl es from these two sections. (Table II-4). Densities of periphyton and living algae were much greater on rock surfaces grazed by *O. zelti* larvae (Fig. II-8). Also, the riffles occupied by *O. zelti* were significantly wider. The mean gradient of *O. zelti* riffles was 5.0% compared to a mean gradient of 6.6% for the upstream riffles. Riffle gradients were generally lower in the

OLIGOPHLEBODES ZELTI

NEOTHREMMA ALICIA

Plate II-1. Scanning electron micrographs of mouthparts of fifth instar *O. zelti* and *N. alicia* showing their scoop-shaped mandibles.

Plate II-2. Scanning electron micrographs of *O. zelti* fifth instar larva mouth opening. Vertical bar lines show the width of the opening (124 μm)

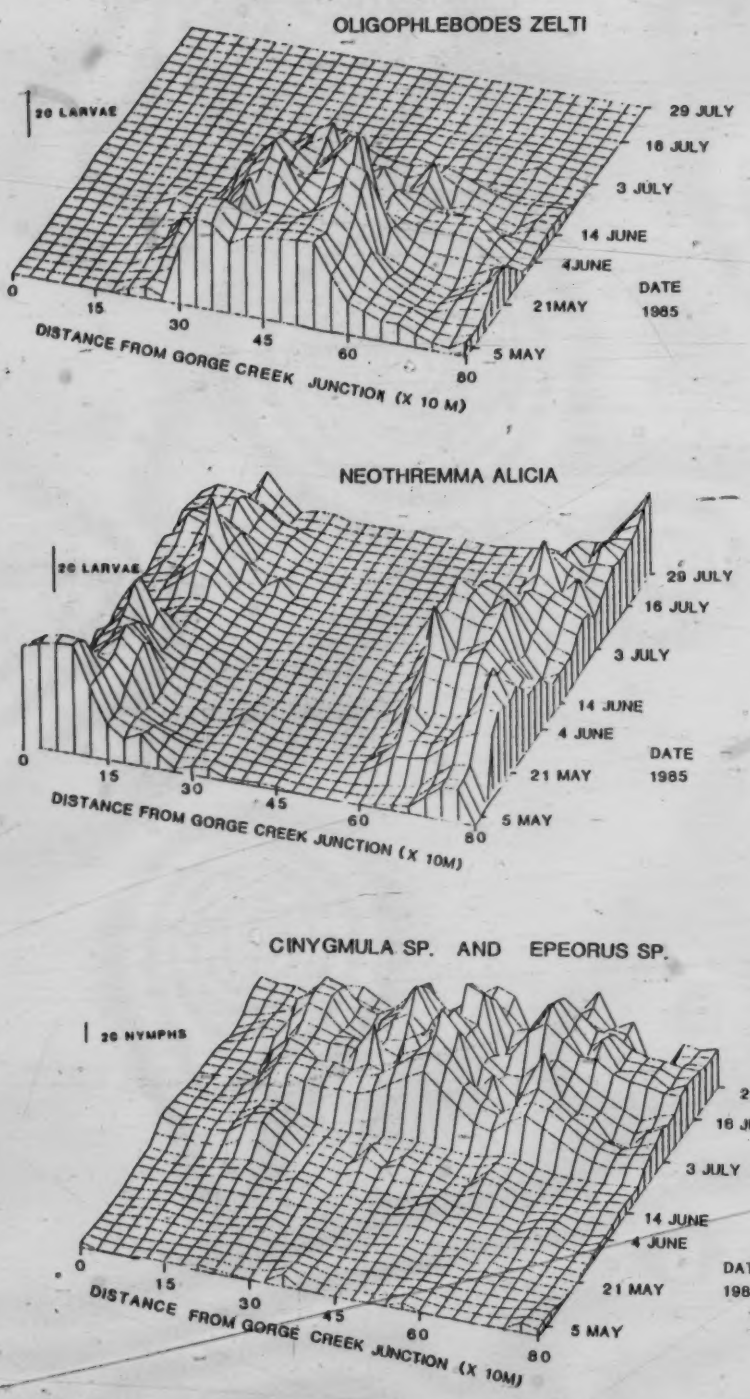


Figure II-7. Distributions of *O. zelti*, *N. alicia Cinygmula* sp. and *Epeorus* sp. within the study area between May and July, 1985. The height of each peak represents the number of larvae or nymphs found on 10 rocks sampled within a particular riffle on one date. Thirty three riffles were sampled on each date. The grid nodes between data points were calculated by interpolating from the eight nearest nodes.

Table II-4. Means and standard deviations for parameters measured from six riffles. Riffles 1-3 are in the mid-section (350-610 m upstream of the Gorge Creek junction) and riffles 4-6 are in the upstream section (610-800 m upstream of the Gorge Creek junction) of the study area. P=Significance values; results of non-parametric Kruskal-Wallis tests to determine if there were any differences among these parameters for the six riffles. *=P<0.05 Total sample size=60 rocks or measurements (10 for each riffle).

| Parameter | Riffles;Mean(SD) | | | | | | P |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | |
| Riffle width (M) | 1.6 (0.2) | 1.6 (0.4) | 1.7 (0.2) | 0.7 (0.1) | 0.9 (0.1) | 1.3 (0.1) | 0.00* |
| Water velocity (cm/sec) | 25 (10) | 18 (4) | 30 (13) | 29 (12) | 27 (11) | 30 (10) | 0.28 |
| Water depth (cm) | 6.0 (1.6) | 6.0 (1.5) | 5.9 (1.3) | 7.1 (0.9) | 6.8 (1.0) | 6.5 (1.3) | 0.07 |
| Chlorophyll *a* ($\mu g/cm^2$) | 1.0 (0.4) | 1.0 (0.9) | 0.7 (0.2) | 0.3 (0.2) | 0.5 (0.3) | 0.4 (0.2) | 0.00* |
| AFDW ($mg/cm^2$) | 1.5 (1.0) | 1.6 (1.6) | 1.1 (0.3) | 0.3 (0.2) | 0.1 (0.1) | 0.4 (0.3) | 0.03* |

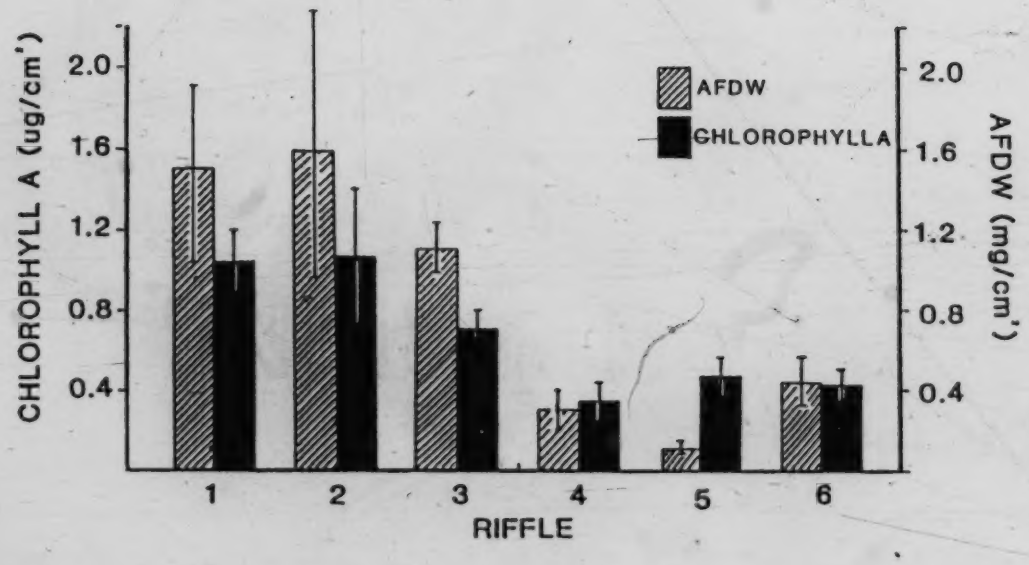


Figure II-8. Mean densities of chlorophyll *a* ($\mu g/cm^2$) and AFDW ($mg/cm^2$) for ten rocks taken from each riffle. Vertical bars represent standard errors. Sampling was done on 28 May, 1985. Riffles 1-3 are in the midsection of the study area (350-610 M upstream of the Gorge Creek junction) and were dominated by *O. zelti* larvae. Riffles 4-6 are further upstream (610-800 M upstream of the Gorge Creek Junction) and were dominated by *N. alicia* larvae.

midsection of the study area (Fig. II-9). Average water velocities were higher in the upstream riffles dominated by *N. alicia* larvae.

Results of correlations between the densities of *N. alicia* and *O. zelti* larvae and living algae, periphyton, other grazers and flow on individual rocks reflect their associations within a riffle (Table II-5). Rocks with zero density of either species of caddis larvae were not used for these analyses. *Neothremma* larvae occurred on rocks throughout the sampling period in 1984 at a mean density of 0.047/cm² (N=50, SD=0.042/cm²). *Oligophlebodes* larvae, because of their life cycles, did not occur in the samples until the end of August when mean densities were 0.058/cm² (N=22, SD=0.058/cm²). *Neothremma* larval densities were not correlated with living algae or periphyton in 1984 though densities of *Oligophlebodes* were correlated with both these parameters. I was mainly interested in associations between the larvae and their food source, and in 1985 only sampled rocks from the mid-section of the study area dominated by *O. zelti*.

Although densities of *O. zelti* were much lower in 1985 (mean=0.029/cm², N=37, SD=0.022/cm²) they were still positively associated with periphyton. They were not correlated with chlorophyll *a*. This is not surprising because the mean chlorophyll *a* density was only 1.07 $\mu$g/cm² (N=39, SD=0.98 $\mu$g/cm²) which is less than 1% the total periphyton density (mean=1.20 mg/cm², N=37, SD=0.92 mg/²cm). The positive association between *O. zelti* and chlorophyll *a* in 1984 was probably due to the increase in larvae and chlorophyll *a* densities over the sampling period. The possibility of temporal trends affecting the results was eliminated in 1985 by reducing the sampling period to 3 weeks.

Densities of *O. zelti* and *N. alicia* larvae were not correlated with water velocities. However, both species occurred only on rocks beneath the highest water velocities in each riffle. I quantified larval abundances and water velocities for rocks in 3 transects across 5 different riffles and found neither *N. alicia* or *O. zelti* larvae occurred in water velocities less than 14 cm/sec. The mean water velocities above rocks sampled in 1985 was 34.4 cm/sec (N=40, SD=18.7 cm/sec). There were no negative correlations between densities of *O. zelti*

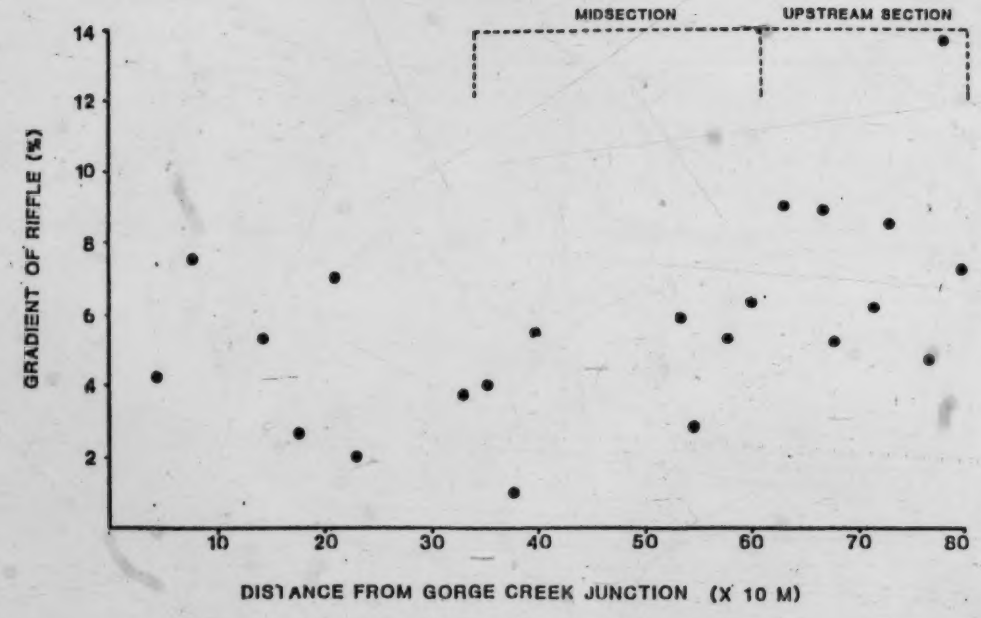


Figure II-9. Riffle gradients within the Dead Horse Creek study area. The midsection (350-610 M upstream of the Gorge Creek junction) was dominated by *O. zelti* larvae and the upstream section (610-800 M upstream of the Gorge Creek junction) was dominated by *N. alicia* larvae.

Table II-5. Summary of the correlation analyses between *O. zelti* and *N. alicia* densities, and the other parameters measured for individual rocks in 1984 and 1985. N = Sample Size, R = Correlation Coefficient, P = Significance (*=P<0.05).

| | | Chl. *a* | | AFDW | | Other Grazers | | Flow | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1984 | 1985 | 1984 | 1985 | 1984 | 1985 | 1984 | 1985 |
| *O. zelti* | N | 21 | 30 | 21 | 34 | 8 | 19 | - | 37 |
| | R | 0.48 | 0.22 | 0.57 | 0.34 | 0.59 | 0.29 | - | -0.17 |
| | P | *0.03 | 0.19 | *0.01 | *0.04 | 0.11 | 0.23 | - | 0.32 |
| *N. alicia* | N | 49 | 12 | 47 | 10 | 38 | - | - | 13 |
| | R | -0.06 | -0.15 | 0.03 | 0.14 | -0.08 | - | - | -0.08 |
| | P | 0.68 | 0.63 | 0.82 | 0.70 | 0.65 | - | - | 0.78 |

or *N. alicia* and other grazers on individual rocks. *Epeorus* sp. and *Cinygmula* sp. (Ephemeroptera: Heptageniidae) were the most common 'other grazers' in Dead Horse Creek (Table II-6). These mayfly nymphs occurred at high densities mainly in the mid section (360 to 610 M upstream of the Gorge Creek junction) of the study area after *O. zelti* pupation (Fig II-7).

Table II-6. Feeding mechanisms for the macro-invertebrates inhabiting rock surfaces in riffles of Dead Horse Creek. Gut analyses were done for 5-10 individuals of each taxa. •=Common taxa.

| Taxa | Feeding Mechanism |
|---|---|
| Order Ephemeroptera | |
| Family Heptageniidae | |
| *Epeorus* sp. | Grazer • |
| *Cinygmula* sp. | Grazer • |
| Family Baetidae | |
| *Baetis* sp. | Grazer |
| Family Siphlonuridae | |
| *Ameletus* sp. | Grazer |
| Family Ephemerellidae | |
| *Drunella coloradensis* | Grazer/Predator |
| Order Trichoptera | |
| Family Rhyacophilidae | |
| *Rhyacophila* sp. | Predator |
| Family Limnephilidae | |
| *Oligophlebodes zelti* | Grazer • |
| *Chyranda centralis* | Shredder |
| *Ecclisoymia maculosa* | Shredder |
| Family Uenoidae | |
| *Neothremma alicia* | Grazer• |
| Family Glossosomatidae | |
| *Anagapetus debilis* | Grazer |
| Family Hydropsychidae | |
| *Parapsyche* sp. | Filter-Feeder |
| Order Plecoptera | |
| Family Chloroperlidae | |
| *Utaperla* sp. | Grazer |

# DISCUSSION

## Life cycles

Life cycles of benthic invertebrates are influenced by temperature (Hynes 1970) and food quantity and quality (Anderson and Cummins 1979). It is difficult to assess these effects separately because water temperature influences most food sources in freshwater environments. Species that display different life cycles in different localities are thought to be responding to environmental variations by changing their growth rates. This life cycle variability has been observed in Alberta for populations of *Cinygmula* sp. (Hartland-Rowe 1964) and *Tipula sacra* (Pritchard 1978). My data suggest that life cycle variablility in response to changes in temperature can be observed over time as well as locality. Temperatures in the study area were much higher in June 1985 than in June 1984. This caused rapid snowmelt, and by 5 June 1985 the entire study area was ice-free. This did not occur until the 21 June in 1984. Life cycle stages recorded in 1985 for the *O. zelti* and *N. alicia* populations occurred 3 weeks earlier than in 1984. For the two year study it was impossible to tell which year was typical, if either. The phenomenon is interesting because life cycles are often reported for species following 1 year of sampling. One should use caution in suggesting a "fixed" life cycle from 1 year of data.

The 2 year life cycle of *N. alicia* in Dead Horse Creek could be a response to low water temperatures. *Neothremma alicia* is a common caddisfly in western mountain streams as far south as Oregon (personal observations). It would be interesting to compare life cycles between these populations, but to my knowledge no life cycle studies of *N. alicia* have been done for these southern locations. The Dead Horse Creek population has a very long fifth instar stage. A similar extended fifth instar stage was found in a nearby population (Dyson Creek) of *Dicoemoecus atripes*, this caddisfly also has a two-year life cycle (Gotceitas and Clifford 1983). Extended fifth instar stages may be caused by low temperatures, which slow rates of growth. Seventy-eight percent of all larval *N. alicia* growth and 65% of all larval *O.*

*zelti* growth occurred during the fifth instar. Any factor affecting life histories through an influence on growth rates would exert its greatest impact during these fifth instar stages.

Although complete life cycles have not been previously reported, adult flight times have been recorded for *N. alicia* and *O. zelti* in Alberta. Nimmo (1971) collected *O. zelti* adults between 14 July and 19 August. I collected adults over about the same period in Dead Horse Creek (between 8 and 31 July). Nimmo collected *N. alicia* adults in Alberta over nearly the entire summer from 22 June to 13 August. The adult flight season in Dead Horse Creek was between 16 July and 31 August. This delay in Dead Horse Creek could be caused by late snow melt and low water temperatures.

**Feeding**

*Oligophlebodes* and *Neothremma* larvae feed mainly on the FPOM within the periphyton and this does not include living algae. Madsen (1972) also found that FPOM was the major food source for grazing stoneflies in a small stream in Denmark. Pennak (1977) suggested that in Rocky Mountain streams 90% of nutrient uptake for benthic organisms was from the non-living fraction of periphyton. Rounick and Winterbourn (1983) conducted radio-tracer experiments and found stream invertebrates fed on the heterotrophic layers of rock surfaces. Recently, Winterbourn *et al.* (1985) suggested that rock surfaces are important sites for the adsorption of dissolved organic matter (DOM), which is utilized by grazing invertebrates. Apparently the concept that grazing macroinvertebrates feed extensively on the living algae of rock surfaces is inaccurate for many streams. The contribution of living algae to the periphyton biomass and to the diets of grazing invertebrates should be assessed before chlorophyll *a* is used to quantify the associations between grazers and their food source.

It is difficult to determine whether periphyton is limiting to the growth of *O. zelti* or *N. alicia* larvae. I could only compare the amount of food consumed to the amount of food present on rock surfaces in Dead Horse Creek riffles. Gose (1966) found that larvae of the

fifth instar *Stenopsyche grisipennis* (Trichoptera) consumed 9-16% of their body weight in periphyton per day over the 4-11°C temperature range. Similar feeding rates were calculated for grazing macroinvertebrates by Rounick and Winterbourn (1983) and Cummins (1973). Assuming a fifth instar *O. zelti* or *N. alicia* larva ingests 16 % of its body weight per day, I calculated that at average densities *O. zelti* larvae ingest 0.60% and *N. alicia* larvae ingest 0.83% of the periphyton biomass on an average rock per day. I did not measure periphyton renewal rates. In a Californian stream, Hart (1981) estimated periphyton renewal had occurred by 2.5 days after grazing. In Dead Horse Creek, periphyton renewal times would have to be greater than 166 days to limit *O. zelti* growth and 120 days to limit *N. alicia* growth. These calculations assume that all the periphyton on a rock is available to the grazing caddis larvae. It is unlikely that other grazers occur at high enough densities to significantly decrease the periphyton available to *O. zelti* or *N. alicia* larvae. However the caddis larvae may only be able to feed on periphyton that is unattached and smaller than the width of their mouths (125 $\mu$m). It would be interesting to divide the periphyton into size fractions and carry out similar calculations.

The components of the periphyton are bound within a mesh of polysaccharide filaments that are secreted by the bacteria (Lock 1983). From the analysis of mouthparts and gut contents, I conclude that grazing *O. zelti* and *N. alicia* larvae would not be capable of selecting particular food items within the periphyton. Changes in larvae's gut contents may reflect changes within the periphyton over time. For example, third and fourth instar *N. alicia* guts contain higher percentages of diatoms. These larvae were taken from the stream between July and September 1984, when stream temperatures were highest. Higher water temperatures increase the production and also the sinking rates of diatoms (Patrick 1977). The increases in chlorophyll *a* in periphyton samples over this time also support the idea that diatom densities were higher. *Oligophlebodes* and *Neothremma* larvae use their spoon-shaped mandibles to scoop FPOM and diatoms into their mouths as they move across the rock surface. They would not be able to select for different food items enmeshed within the

periphyton matrix.

**Micro-distribution within study area**

The limited distribution of the *O. zelti* population in Dead Horse Creek may be due to many factors. Altitudinal zonation has previously been observed for Trichoptera species within Rocky Mountain streams (Mecom 1972 and Ward 1981). This is not a good explanation for the restricted *O. zelti* distribution in Dead Horse Creek because the altitude changes by only 32 m over the 360 m section the larvae occur in. It is unlikely that a species altitudinal preferences would be limited to a 32 m range. Short adult flight distances could be limiting the *O. zelti* population's dispersal. Flight patterns of Trichoptera adults have been shown to influence the distribution of the larvae (Statzner 1978). *Oligophlebodes* adults and larvae or both could be actively selecting the rocks within the mid-section of the study area to lay eggs (adults) or colonize (larvae). These rocks have significantly higher densities of living algae and periphyton than rocks within the riffles upstream. Riffles upstream of the *O. zelti* riffles are steeper with higher water velocities. Stevensson (1984) showed that rates of sedimentation and accumulation of organic matter increase with slight decreases in water velocities. A similar negative association between water velocity and periphyton densities was observed by Liaw and Macrimmon (1978).

*Neothremma alicia* larvae have been reported in two distributional studies of Trichoptera larvae in the St. Vrain River, Colorado. Mecom (1972) found that 90.68% of the Trichoptera larvae at an altitude of 2650 m were *N. alicia* and Ward (1982) collected *N. alicia* larvae in the same river between altitudes 2200 and 3400 m. At higher latitudes *N. alicia* may be found at lower elevations: the population I studied in Dead Horse Creek occurred at an altitude of 1500 m. Mecom (1972) did mention that he never found *N. alicia* larvae at water temperatures exceeding 11°C which is approximately the maximum water temperature I recorded in Dead Horse Creek.

*Oligophlebodes zelti* has a 1 year life cycle, higher growth and production rates and occurs in the lower velocity riffles of Dead Horse Creek where periphyton (food) densities are higher. *Neothremma alicia* has a 2 year life cycle, slower growth rates and occurs in riffles with lower periphyton densities. The larval morphology of each species is also suited to their different habitats. *Oligophlebodes* has a wide coarse-grained case and *Neothremma* has a long narrow case that is covered in an external layer of silk. Riffles in the upstream section of the study area dominated by *N. alicia* larvae had higher gradients and water velocities though these results were not significant. There was little overlap between the distributions of the species, and I did not attempt to investigate the possibility of competition between them.

**Micro-distribution within riffles**

Patterns of benthic invertebrate micro-distributions within small segments of streams or lakes have been investigated using two different approaches. One approach is to manipulate a variable experimentally and investigate the resulting (if any) changes in invertebrate distributions. There is usually an attempt to keep all other variables constant. Periphyton can be experimentally manipulated by placing bare substrates in the stream for varying lengths of time prior to the experiment, and this technique is used later in my study (see Chapter III). The second approach is to quantify and attempt to correlate densities of invertebrates and environmental variables within a specified sampling unit. Significant correlations can be interpreted only as an association between invertebrate densities and the measured variable. It is not known if the cause of this association is the result of the measured variable's direct influence on invertebrate distributions or the outcome of responses to other unmeasured variables. The possibility of recognizing a spurious correlation is increased when many variables are quantified and tested for possible correlations.

Periphyton densities have been negatively (Douglas 1958, Doremus and Harem 1971) and positively (McAuliffe 1983) correlated with grazer densities. The conflict arises because each point in a correlation is the product of two opposing processes: the influence of

periphyton on a grazer's distribution and the impact of the grazer on periphyton densities. If grazer populations significantly deplete periphyton, grazer and periphyton densities may be negatively correlated even when periphyton influences the micro-distribution of grazers. In Dead Horse Creek, the mean densities of *O. zelti* and *N. alicia* on rocks with larvae were 0.058/cm² and 0.047/cm² respectively. These values are lower than grazer densities from studies that have reported grazers significantly deplete the periphyton biomass in streams. Lamberti and Resh (1983) showed high densities (0.413/cm²) of *Helicopsyche borealis* (Trichoptera: Helicopsychidae) reduced periphyton biomass by 90% over 9 days. In contrast, Kedhe and Wilhm (1972) found low densities (0.012/cm²) of *Phsya gyrina* (Mollusca) did not effect periphyton biomass in laboratory streams. The possibility that grazers are effecting periphyton densities (and hence the correlations) is not a problem in this study because caddis larvae occurred at low densities and probably ingested less than 1% of the periphyton on an average rock per day.

A major determinant for the presence or absence of correlations between variables is the size of the sampling unit. Many correlative studies have been criticized for using sampling units with no biological relevance, for example the 0.08 m surber sampler. The sampling unit in my study was the top and sides of one rock selected randomly from high water flow riffle areas of Dead Horse Creek. The advantages of using rocks as the sampling unit in freshwater ecological studies have been reviewed by Fox (1977). In this study, I assumed that there are large energy outputs and risks associated with moving between rocks for larvae of the two species. If this is true, I would expect local conditions affecting individual rocks to be paramount in affecting the larvae's distributions.

The conditions I investigated were living algae (chlorophyll *a*), periphyton (AFDW), water velocity and the presence of other grazers. In 1985, densities of chlorophyll *a* were not correlated with either *O. zelti* or *N. alicia* larvae. Chlorophyll *a* can be multiplied by 67 to give a rough estimate of the biomass of living algae within the periphyton (American Public Health Association 1980). Living algae only constituted approximately 6% of the periphyton

on rock surfaces in Dead Horse Creek and is unlikely to influence the distributions of grazers. In more open streams the algal component of the periphyton is probably greater. The mean chlorophyll *a* density in Dead Horse Creek was 1.07 $\mu g/cm^2$ (1985 data), which is lower than mean values reported for other streams at similar latitudes (2-3 $\mu g$, Lock 1983). However Lamberti and Resh (1983) reported chlorophyll *a* densities of only 1.44 $\mu g/cm^2$ during Summer in a Californian stream. The average periphyton (AFDW) density in this Californian stream was 0.97 $mg/cm^2$, hence algal biomass constituted approximately 9.9% of the periphyton which is very similar to the value calculated for Dead Horse Creek.

The Autotrophic Index (AI), which is the ratio of chlorophyll *a* to AFDW, is often used to quantify the auto/heterotrophic nature of periphyton samples. Weitzel (1979) states that AI values greater than 100 reflect heterotrophic conditions. The average AI for periphyton samples from Dead Horse Creek was 2607 in 1984 and 1625 in 1985. Similarly AI values from the stream studied by Lamberti and Resh (1983) were very high; 5142 (winter) and 687.9 (summer). Even in laboratory streams under high light intensities and with high chlorophyll *a* densities (21.1 $\mu g/cm$), the AI value was 123.2 (Sumner and McIntire 1982). If the ratio of chlorophyll *a* to living algae biomass is 67, then living algae would have to constitute over 67% of the periphyton biomass on rocks for the periphyton to be considered autotrophic by Weitzel's criteria.

There was a significant correlation between densities of periphyton (AFDW) and *O. zelti* larvae on individual rocks in 1984 and 1985. Neither was correlated with any other variables measured indicating there was a direct association between grazing *O. zelti* larvae and their periphyton food source. This could be caused by larvae selectively colonizing (or remaining for longer periods) on rocks with higher periphyton levels. Hart (1981) and Kohler (1984) showed that grazing benthic invertebrates will spend longer periods on patches of substrate with higher periphyton densities. These studies suggest natural selection operating to favour behaviours that result in efficient location of a limiting periphyton food resource.

If there is an overabundance of food available in Dead Horse Creek and *O. zelti* larvae are not capable of selecting for variations in food quality, why do they graze on rocks with more periphyton? I do not think food must reach levels that limit growth before selection pressures occur to favour the evolution of efficient feeding behaviours. If rate of ingestion affects growth rates (and this in turn affects an individual's fitness) these behaviours will evolve when there is a range of food availability. *Oligophlebodes* in Dead Horse Creek appear to have evolved behaviours that distribute the larvae on rocks with high densities of periphyton. *Neothremma* larvae were not associated with their food source and occurred in riffles where quantities of food were significantly lower. The *N. alicia* population had a longer life cycle and slower growth rates than that of the *O. zelti* population. *Neothremma alicia* larvae occur in riffles with higher water velocities than *O. zelti* larvae and are morphologically suited to these conditions because the larval case is very streamlined. It seems likely that *N. alicia* fitness would be more influenced by the position of larvae in the stream with respect to water velocities than quantities of food.

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# III. THE EFFECTS OF PERIPHYTON MANIPULATIONS ON THE MICRO-DISTRIBUTION OF OLIGOPHLEBODES ZELTI, NEOTHREMMA ALICIA AND EPEORUS SP.

## INTRODUCTION

An animal's foraging behaviour can be described by general models if the animal forages to maximize its net rate of energy gain in an environment where food is patchily distributed (for reviews see Pyke *et al.* 1977, Townsend and Hughes 1981). These models predict that the amount of time an animal allocates to a food patch will be positively correlated with the energetic yield of that patch (e.g. Charnov 1976, Pyke 1978). If there is a correlation, the distribution of the animal will be closely associated with the density or quality of its food patches. In streams, grazing macroinvertebrates feed by scraping periphyton from rock surfaces (Cummins 1973). Periphyton is a complex community of fungi, bacteria, algae, inorganic and organic particulate matter (Wetzel 1983). This complex is enmeshed in polysaccharide filaments secreted by bacteria (Lock 1983). Evidence from gut contents (Short 1983) and mouthpart structures (e.g. Cummins and Klug 1979, Lamberti and Moore 1984) indicate grazers are generalist feeders; that is, they do not select specific components of the periphyton. Therefore, if grazers are foraging to maximize net rates of energy gain, grazer micro-distributions will be closely associated with periphyton densities.

Periphyton densities vary (are patchily distributed) on different spatial scales within a stream. For example, periphyton densities vary between riffles (see Chapter II), between rocks (Jones 1978) and between areas within a rock (Stevensson 1984). Periphyton densities can be manipulated experimentally on these spatial scales, and the micro-distributions of grazers can be accurately quantified on the same scale. Investigators usually assume all grazer movements are related to the periphyton, because time budgets (Hart and Resh 1980) and gut volume analyses (Moore 1977) indicate that grazers spend most of the time feeding.

Previous studies have demonstrated a close association between patches of periphyton densities and movement or micro-distributions of some grazing macroinvertebrates. Hart (1981) and Kohler (1984) investigated movement patterns for the grazing caddis larva *Dicoesmoecus gilvipes* (Trichoptera: Limnephilidae) and the mayfly nymph *Baetis tricaudatus* (Ephemeroptera: Baetidae) respectively. They showed that grazers will respond to experimental manipulations of periphyton density within artificial substrates by spending more time on periphyton patches versus bare areas. Grazing macroinvertebrates will also respond to variations in periphyton densities between rocks by selectively colonizing rocks with more periphyton (Lamberti and Resh 1983, McAuliffe 1983). This evidence for the influence of periphyton on the micro-distributions of grazers in streams supports the premise that grazers forage to maximize net rates of energy gain.

Most of the reported studies of grazer-periphyton interactions in streams have been done in situations where periphyton densities are low and grazer densities are high. Lamberti and Resh (1983) showed grazers significantly depleted the periphyton standing crop, and McAuliffe (1983) suggested grazers competed for a limiting periphyton food resource. In Dead Horse Creek, the periphyton on an average rock is much more than the grazer populations consume although periphyton densities do vary greatly between rocks (see Chapter II).

My study tests the hypothesis that the patchy distribution of periphyton densities in Dead Horse Creek influences the micro-distribution of *O. zelti*, *N. alicia* and *Epeorus*. I manipulated periphyton densities on two spatial scales: between individual rocks and within tiles. I then quantified the micro-distributions of grazers on both these scales. In the first two experiments, Periphyton Density 1 and 2 (PD1 and PD2), rocks were randomly assigned to one of three treatments (periphyton densities): bare, depleted and natural. Grazer abundances were quantified on all rocks every 3 days throughout the experiments. To investigate the effect of patchy periphyton densities on individual tile surfaces, I scraped the periphyton from different-sized areas on tiles (Patch Size experiment). I then quantified the

micro-distribution of *N. alicia* larvae on bare and periphyton-covered patches on the tiles surfaces. These experiments were designed to quantify the effects of periphyton density manipulations, at different spatial scales, on grazer micro-distribution in Dead Horse Creek. The aim was to assess whether patchily distributed periphyton can influence grazer micro-distributions in a stream where average periphyton densities appear not to be limiting (see Chapter II) to grazer populations.

## METHODS

The study was conducted in riffles of Dead Horse Creek from May-August 1985. Over this time, I measured stream discharge and water temperatures daily. Dead Horse Creek drains an area of 2.02 $km^2$ and the stream's discharge ranged from 0.026 $m^3$/sec in late May to 0.004 $m^3$/sec in early August. A detailed description of Dead Horse Creek is given in Chapter II. All study riffles were 10-20 m long, approximately 1.1 m wide and had an average water depth of 5.9 cm. The dominant grazing insects on rock surfaces in these riffles were *Oligophlebodes zelti* Nimmo (Trichoptera: Limnephilidae), *Neothremma alicia* Banks (Trichoptera: Uenoidae) and *Epeorus* sp. (Ephemeroptera: Heptageniidae).

### Periphyton Density Experiments

Two experiments were done to investigate the influence of periphyton densities on the micro-distribution of *O. zelti*, *N. alicia* and *Epeorus* sp. between rocks in Dead Horse Creek riffles. Periphyton Density experiment (PD1) was continued for 51 days (9 June-30 July 1985) and Periphyton Density experiment 2 (PD2) was conducted for 28 days (6 July-3 August 1985). There were three periphyton densities (treatments) in each experiment; bare, depleted and natural. The replicates within treatments were individual rocks. For the depleted treatment, I removed 16 rocks from each study riffle and thoroughly scraped the periphyton from the tops and sides of each rock. These rocks were replaced in the study riffles 31 days before the beginning of PD1 and 44 days before PD2. For the bare treatment,

I removed, and scraped an additional 12 rocks from the study riffles. These rocks were replaced in their original riffle position at the beginning of the experiments. Rocks that were left unscraped formed the natural periphyton density treatments.

Before starting the experiments, I investigated whether there were differences in grazer abundances between rocks before periphyton manipulations. Macroinvertebrates were removed from randomly selected rocks within the study riffles and the position of each rock was mapped on a grid. Abundance of macroinvertebrates on individual rocks was monitored after 2 days. Each rock was raised carefully from the substrate, all macroinvertebrates were identified and counted and the rock was replaced in its original position. I randomly assigned half the rocks used in this test to the bare treatment and the other half to the natural treatment. Rocks destined for the bare treatment were removed, scraped and then replaced in exactly the same position in the riffle. This meant that any differences between macroinvertebrate abundances on bare and natural treatment rocks during the experiments could be attributed to periphyton manipulations and not riffle position or water velocities.

I began each experiment by removing all macroinvertebrates from the depleted and natural treatment rocks and then added the positions of the depleted rocks to the riffle grid. The grid of all rock positions allowed me to monitor the abundance of macroinvertebrates on individual rocks in each treatment throughout the experiment. Abundances of macroinvertebrates on all rocks were monitored 2, 3, and 4 days later and then every 3 days until the end of the experiment. Water velocities immediately upstream of each rock were measured to check that there were no differences in water velocities among treatments.

Kruskal-Wallis tests were used to determine whether there were any differences in abundance of *O. zelti*, *N. alicia* or *Epeorus* sp. among treatments on each day monitored. Separate tests were done for *O. zelti* and *Epeorus* sp. during PD1 and for *N. alicia* and *Epeorus* sp. during PD2. These taxa dominated the populations of macroinvertebrates on treatment rocks in the experiments. *Oligophlebodes* abundances were only tested for the first 10 days of PD1 because these larvae began to pupate. I also investigated the distribution of

*N. alicia*, *O. zelti* and *Epeorus* on rocks within treatments using the Chi-Square test to determine if the variance to mean ratios reflected random, regular or contagious distributions (Elliott 1977).

**Patch Size Experiment**

Unglazed clay tiles (19cm x 6cm x 1cm) were used to investigate the influence of periphyton patch size on the micro-distribution of *N. alicia* larvae. Periphyton was scraped from tiles to make different size patches for each treatment. The three treatments (patch sizes) were full, half and quarter of the tile top surface. The use of tiles instead of natural substrates allowed for uniformity of patch size and also surface texture between replicates for each treatment. Periphyton had been accumulating on tiles used in this experiment for 75 days. For the full treatment, tiles were left unscraped; for the half treatment, the periphyton from one half the tile was scraped; and for the quarter treatment, periphyton was scraped from the first and third quarter of the tile. There were five replicates (tiles) for each treatment. Treatment tiles were placed randomly in the study riffle. The position of each tile was mapped onto a grid, and the abundance of *N. alicia* was monitored for 2 days on tiles and on periphyton patches within tiles. To monitor abundance, each tile was carefully raised from the substrate and all macroinvertebrates were immediately identified and counted. The positions of all *N. alicia* larvae on periphyton patches or bare areas were also recorded. The water velocity immediately upstream of each tile was measured at the completion of the experiment. A Mann-Whitney test was done to determine if there were differences between micro-distribution of *N. alicia* larvae on bare areas and periphyton patches for the half and quarter treatment tiles. I used the Kruskal-Wallis test to determine whether there were any significant differences in the abundances of *N. alicia* larvae between treatments.

**Periphyton Accumulations**

Periphyton was quantified to investigate its accumulation on rocks and tiles in all experiments. The periphyton on the tops and sides of the rocks or tiles was analysed using chlorophyll *a* and ash free dry weight (AFDW) analyses. Chlorophyll *a* analysis measures living algae and AFDW measures the total periphyton biomass on a rock. Because grazers are generalist feeders, AFDW is a better measure of grazer food resources than chlorophyll *a*. However, by doing both analyses, the autotrophic: heterotrophic nature of the periphyton can be assessed. The periphyton from the tops and sides of the rock or tile was scraped into a flask containing filtered stream water and two 10 ml subsamples were taken. Each subsample was filtered onto a 2.4 cm glass fibre filter (Whatman GF/C) using a Nalge hand pump. The filters were placed in airtight sealable petri dishes and frozen. Before freezing, magnesium carbonate was sprinkled onto the filters destined for chlorophyll *a* analysis to prevent acidification of the algae. The amount of chlorophyll *a* was determined within 4 weeks using the acetone extraction method (Moss 1967a, b). Each filter was homogenised in 90% acetone for 60 seconds with a polytrol sonicator. Samples were stored in the dark at 4°C for 24 hours. A Pye Unicam (350/550) spectrophotometer was used to measure absorbance of the resulting chlorophyll *a* extract.

The other subsample was dried at 60°C for 24 hours, cooled in a desiccator and weighed to the nearest 0.01 mg using a Cahn gram electrobalance. This subsample was then placed in a muffle furnace for 4 hours at 550°C, cooled and reweighed. The difference between the "ashed" and dried weights is equal to the biomass of periphyton in each subsample, because all organic matter is combusted over 4 hours at 550°C (Wetzel and Likens 1979). The surface area of the top and sides of each rock was measured by carefully wrapping them in aluminium foil. When all pieces of the foil were in direct contact with the rock they were removed and pressed flat. Surface area of the foil was measured using a Pico polar compensating planimeter. Density of living algae ($\mu$g chlorophyll *a*/cm$^2$) and periphyton (mg AFDW/cm$^2$) were calculated using the ratio of subsample to periphyton

sample volume and the rock surface area.

Periphyton accumulation was quantified on depleted rocks before the beginning of the PD1 and PD2 (see Fig. III-1). Periphyton from two rocks was analysed on each sampling date. During the experiments, I quantified the accumulation of periphyton on two rocks from each treatment on days 16, 28 and 42 of PD1 and on day 14 of PD2. These rocks were not returned to the stream. Therefore, the number of replicates for each treatment decreased from 12 to 6 in PD1 and from 10 to 8 in PD2. Periphyton on an additional two rocks from each treatment was analysed at the end of each experiment. Periphyton accumulation was also quantified on tiles prior to the Patch Size experiment. The tiles were placed in a riffle on 15 May 1985 and the periphyton was scraped and analysed from three tiles 5, 10, 15 and then every 10 days thereafter until the end of the experiment.

## RESULTS

### Periphyton Density 1

Before the experiments began, there were no differences between the abundance of *O. zelti* larvae on rocks assigned to the natural and bare treatments (Table III-1). These rocks were replaced in their original positions in the riffles after periphyton manipulations; hence any difference in *O. zelti* abundance between natural and bare treatments can be attributed to different periphyton densities. Within treatments, *O. zelti* larvae were randomly distributed between rocks (Fig. III-2). The mean abundance of *O. zelti* larvae was significantly different among treatments on days 2 and 4. On days 3 and 7, *Oligophlebodes* larval abundances were almost significantly different between treatments ($p=0.08$ for both days, Fig. III-3). On all days monitored, the mean abundance of *O. zelti* larvae was greater on natural than on depleted and bare rocks. For the first 10 days of the experiment, 41.6% of all macroinvertebrates on natural rocks were *O. zelti* larvae (Table III-2).

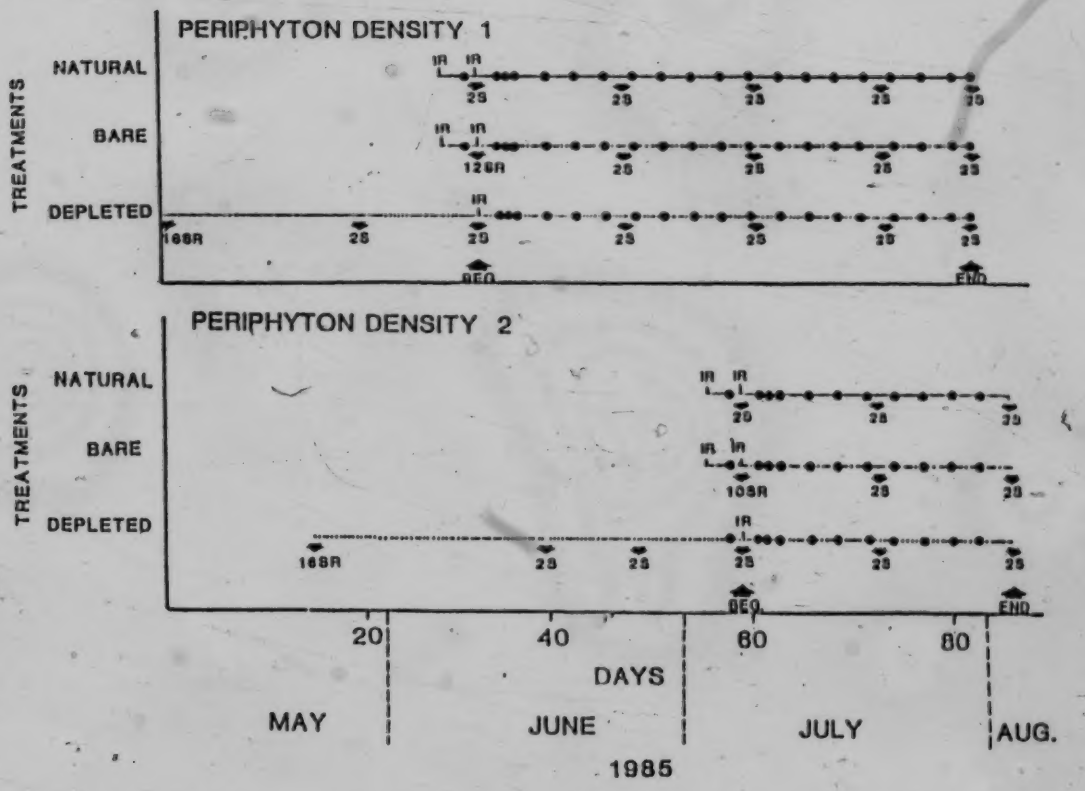


Figure III-1. Sampling schedule to quantify periphyton accumulation and macroinvertebrate abundances on treatments (natural, depleted and bare) in the Periphyton Density experiments. SR = number of rocks that were removed, scraped and replaced in the experimental riffles. S = number of rocks that were removed from the riffle, scraped and not replaced. IR = all macroinvertebrates were removed from the rock surface then the rocks were replaced in the same positon within the riffle. Closed circles indicate the dates macroinvertebrate abundances were monitored for rocks in each treatment. BEG and END are the dates each experiment began and ended.

Table III-1. Results of Mann-Whitney tests to determine if there were differences between abundances of caddis larvae colonizing rocks before experimental periphyton manipulations. A= rocks destined for natural treatments. B = rocks destined for bare treatments. NS = no significant difference in mean abundance ($P>0.05$) .

| | Periphyton Density 1. *O. zelti* | | | Periphyton Density 2 *N. alicia* | | |
|---|---|---|---|---|---|---|
| | Sample size | Mean | Standard deviation | Sample size | Mean | Standard deviation |
| A | 12 | 2.0 | 2.4 | 10 | 3.3 | 2.7 |
| B | 12 | 1.6 | 1.7 | 10 | 2.2 | 1.9 |
| | | NS | | | NS | |

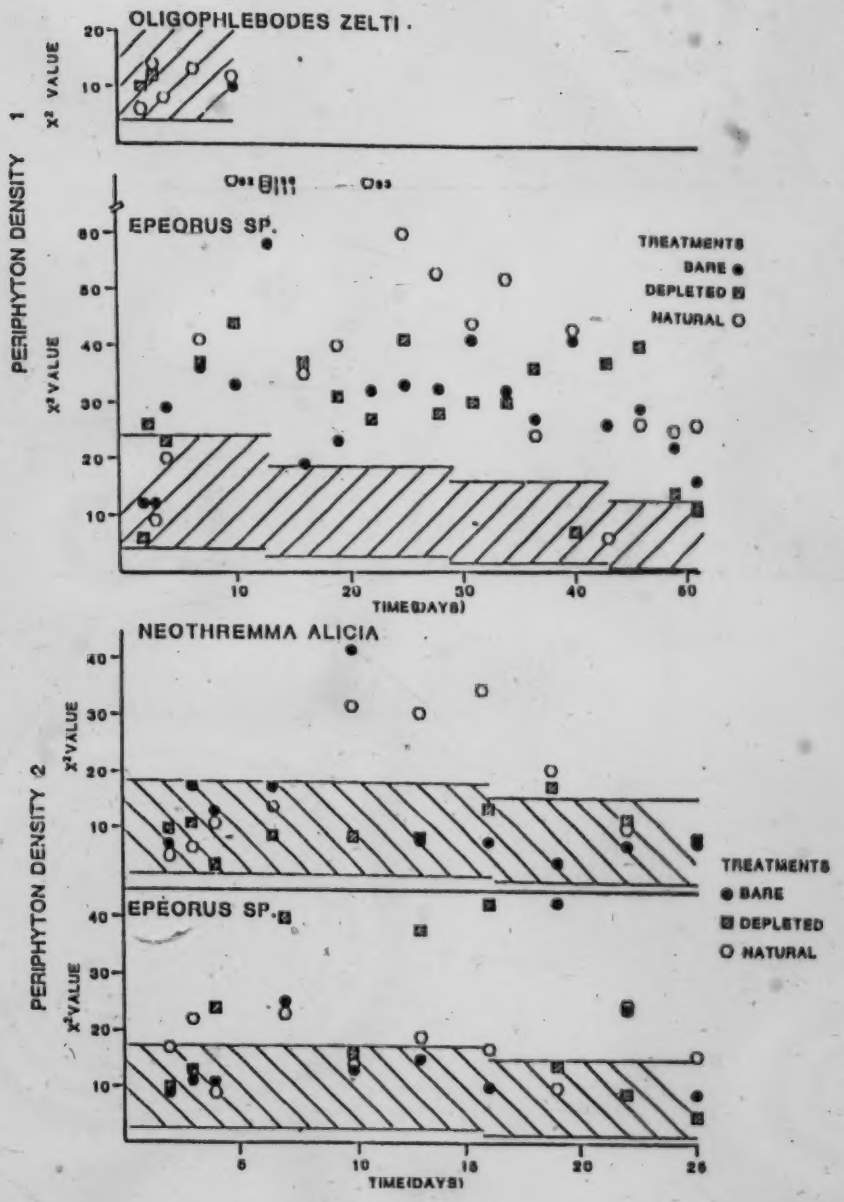


Figure. III-2. Periphyton Density 1 and 2.—
Distribution of *O. zelti* and *N. alicia* larvae and *Epeorus* sp. nymphs between rocks within treatments. $X^2$ value is a function of the Index of Dispersion (variance to mean ratio) that has a $X^2$ distribution (Elliott 1977). Hatched areas represent values for $X^2$ when the animals are randomly distributed between rocks within each treatment. $X^2$ values above the hatched areas indicate the animals are contagiously distributed. The distribution of *O. zelti* within treatments is only analysed for the first 10 days of PD1 because *O. zelti* larvae began to pupate after this time.

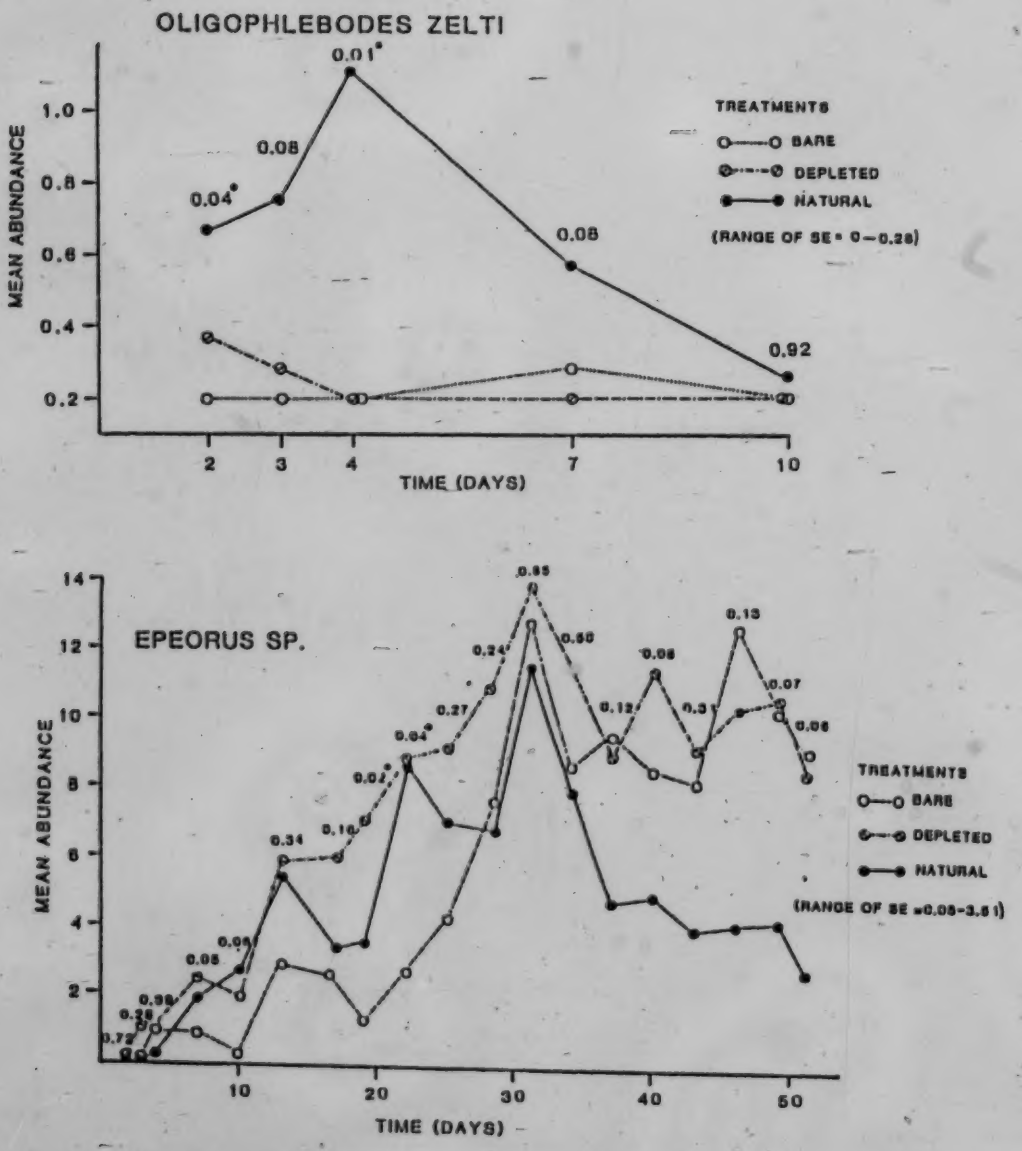


Figure III-3. Periphyton Density 1.
Mean abundance of *O. zelti* larvae on treatment rocks for days 2, 3, 4, 7 and 10 and *Epeorus* sp. nymphs for all sampling dates. Above each sampling date are significance values from non-parametric Kruskal-Wallis tests to determine if there are differences in *O. zelti* or *Epeorus* sp. abundances among treatments. * = $p < 0.05$ Sample sizes are twelve (for each treatment) for sampling days 2 to 13, ten for sampling days 16 to 28, 8 for sampling days 31 to 42 and six for sampling days 45 to 51.

Table III-2. Percentage composition of the grazing macroinvertebrate populations on rock surfaces in each treatment during PD1 and PD2. PD1 is divided into two groups of monitoring dates: The first group for dates that *O. zelti* larvae occurred in the riffle (Day 1-10) and the second group for dates after the *O. zelti* larvae had pupated (Day 11-51). Number of monitoring dates between Day 1 and Day 10 was 5 and between Day 11 and Day 51 was 15 for PD1. Number of monitoring dates for PD2 was 10. SD=Standard deviation.

| Treatments | Bare Mean (SD) | Depleted Mean (SD) | Natural Mean (SD) |
|---|---|---|---|
| PD1 | | | |
| Day 1-Day 10 | | | |
| *O. zelti* | 0.9 ( 2.0) | 4.0 ( 5.6) | 41.6 (29.1) |
| *Epeorus* sp. | 46.0 (19.7) | 55.0 (20.0) | 34.5 (29.0) |
| Day 11-Day 51 | | | |
| *Epeorus* sp. | 83.8 (11.5) | 91.2 ( 8.0) | 81.9 (10.7) |
| PD2 | | | |
| Day 1-Day 28 | | | |
| *N. alicia* | 16.2 (12.7) | 9.4 (4.2) | 19.3 (10.6) |
| *Epeorus* sp. | 54.6 (25.6) | 66.1 (8.9) | 46.0 ( 8.3) |

The distribution of *Epeorus* nymphs on rocks within treatments was contagious (Fig. III-2). There were no significant differences in the mean abundance of *Epeorus* nymphs between treatments for 15 of the 17 days tested (Fig. III-3). The mean abundance of *Epeorus* was generally highest on the depleted periphyton rocks. For the first 31 days of the experiment, *Epeorus* abundance increased in all treatments. At this time (June) all nymphs were very small and the increasing abundances were probably caused by the hatching of an *Epeorus* cohort. The contagious distribution of *Epeorus* nymphs could be a life cycle phenomenon; aggregative behaviour of small stonefly nymphs was observed by Hidrew *et al.* (1980). After 31 days, *Epeorus* abundances on depleted and bare rocks remained at about 11 nymphs per rock but on natural rocks *Epeorus* abundances decreased (Fig. III-2). *Epeorus* was the most abundant macroinvertebrate on all treatments in this experiment (Table III-2).

**Periphyton Density 2**

*Neothremma* larvae were generally randomly distributed between rocks within the depleted and bare treatments, but on natural rocks *N. alicia* larvae were contagiously distributed after day 7 of the experiment (Fig. III-2). This indicates that *N. alicia* larvae tended to cluster on a few natural rocks and randomly disperse among scraped rocks with lower periphyton densities (depleted and bare treatments). There were no significant differences between abundances of *N. alicia* larvae colonizing treatments on any of the days tested (Fig. III-4). *Neothremma* larvae comprised between 9.4 and 19.3% of all macroinvertebrates on rock surfaces in the three treatments (Table III-2).

Within each treatment, the distributions of *Epeorus* sp. nymphs between rocks fluctuated from random to contagious (Fig. III-2). Contagious distributions were less pronounced than in PD1 and this supports the idea that aggregations may be an early life stage phenomenon. Alternatively, aggregations of nymphs on a few rocks within treatments may reflect a response by *Epeorus* to an unmeasured variable. The mean abundances of *Epeorus* nymphs were significantly different between treatments on days 2, 4, 7, 10, 13 and

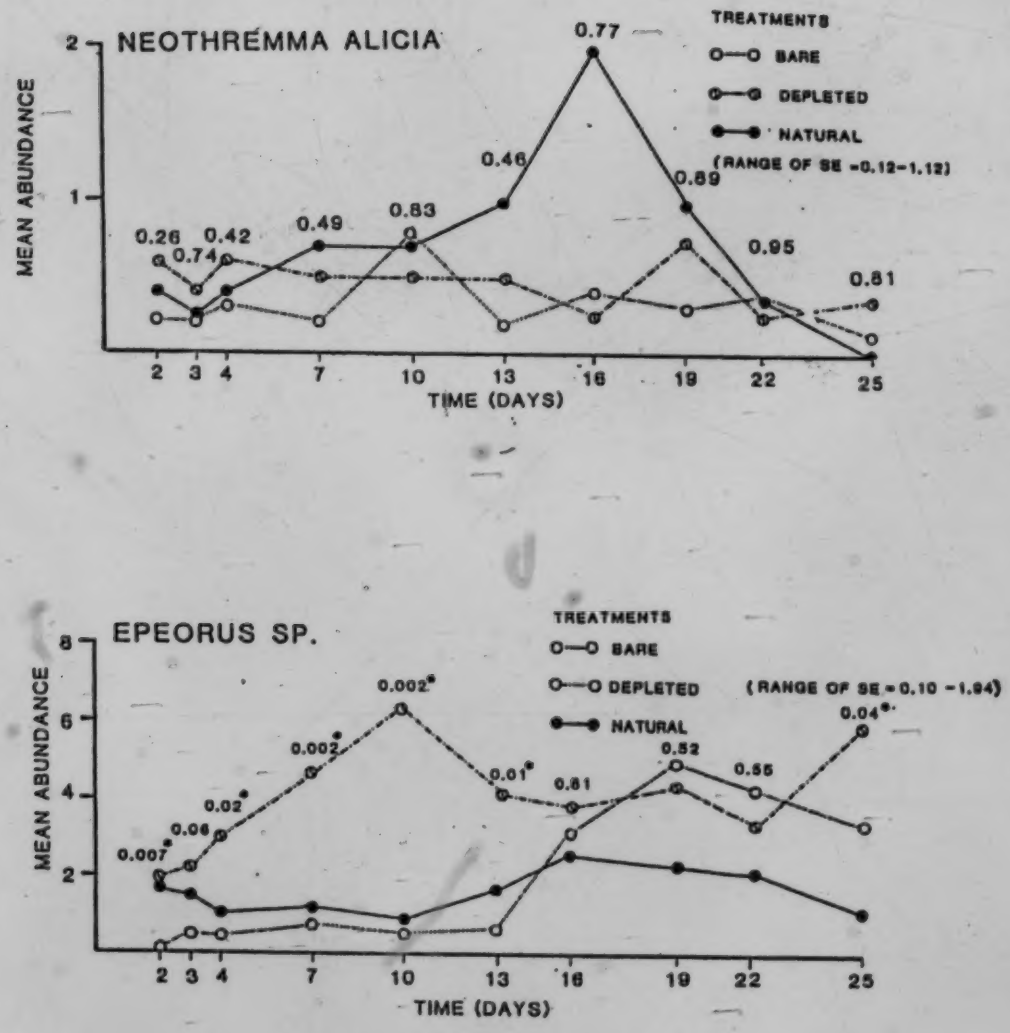


Figure III-4. Periphyton Density 2.
Mean abundance of *N. alicia* larvae and *Epeorus* sp. nymphs on treatment rocks for all sampling dates. Above each sampling date are significance values from non-parametric Kruskal-Wallis tests to determine if there are differences in abundances for each taxa between treatments. * = $p < 0.05$. Sample sizes for each treatment are ten for sampling days 2 to 13 and eight for sampling days 14 to 28.

25 of the experiment (Fig. III-4). On these dates, mean abundance was highest in the depleted treatments; this response was also observed in PD1. *Epeorus* nymphs rapidly colonized depleted rocks, and by day 10 abundance had reached a peak level of approximately four nymphs per rock. Abundance of *Epeorus* nymphs remained low on bare rocks until day 13 of the experiment and then increased rapidly. Mean abundance of *Epeorus* nymphs on natural rocks fluctuated between one and three nymphs throughout the experiment, which indicates that densities of *Epeorus* sp. nymphs were constant in the study riffle over this time. As in PD1, *Epeorus* sp. dominated the grazing populations on all treatments (Table III-2).

**Patch Size Experiment**

*Neothremma alicia* larvae constituted 82% of all macroinvertebrates monitored on day 1 and 73% on day 2 of the experiment. There were no significant differences in the abundances of *N. alicia* larvae between treatments (Table III-3). Colonizing *N. alicia* larvae did not appear to prefer unscraped (full) tiles over scraped tiles that had half as much periphyton (half and quarter treatments). The size of periphyton patches did not influence the micro-distribution of *N. alicia* larvae between tiles. Within a tile, there were significant differences between *N. alicia* larvae abundance on periphyton patches and bare areas for both days of the experiment (Table III-4). *Neothremma alicia* larvae were found almost exclusively on the periphyton patches within the half and quarter treatment tiles. This is probably not a response to the larvae's need to cling to a rough surface. The clay tiles used had a rough texture, and I observed *N. alicia* clinging to smooth glass surfaces under similar water velocites in an artificial stream.

**Periphyton Accumulations**

At the beginning of PD1 and PD2, periphyton and living algae densities on the depleted treatment rocks were still very low compared to natural rocks (Figs. III-5 and III-6). After 14 days there were no differences between mean chlorophyll *a* (Fig. III-6) or

Table III-3. Results of Kruskal-Wallis tests to determine if there were differences between the mean abundance of *N. alicia* larvae on treatment tiles during the Patch Size experiment. There were five replicates for each treatment. KW = Kruskal-Wallis statistic, NS = no significant difference ($P > 0.05$)

| Treatment | Day 1 | | Day 2 | |
|---|---|---|---|---|
| | Mean (no./tile) | Standard deviation | Mean (no./tile) | Standard deviation |
| Full | 2.2 | 1.9 | 6.0 | 5.6 |
| Half | 3.0 | 1.9 | 6.0 | 5.6 |
| Quarter | 5.2 | 4.2 | 2.6 | 1.8 |
| KW | 1.6(NS) | | 4.0(NS) | |

Table III-4. Results of Mann-Whitney tests to determine if there were differences between mean abundance of *N. alicia* larvae on periphyton patches and bare areas of treatment tiles during the Patch Size experiment. Sample size=10 bare areas and 10 patches. P = Significance value. * = $P < 0.05$.

| | Day 1 | | Day 2 | |
|---|---|---|---|---|
| | Mean no./tile | Standard Deviation | Mean no./tile | Standard Deviation |
| Bare | 0.8 | 0.6 | 0.5 | 0.5 |
| Patches | 4.0 | 2.9 | 2.4 | 2.0 |
| P | 0.009* | | 0.009* | |

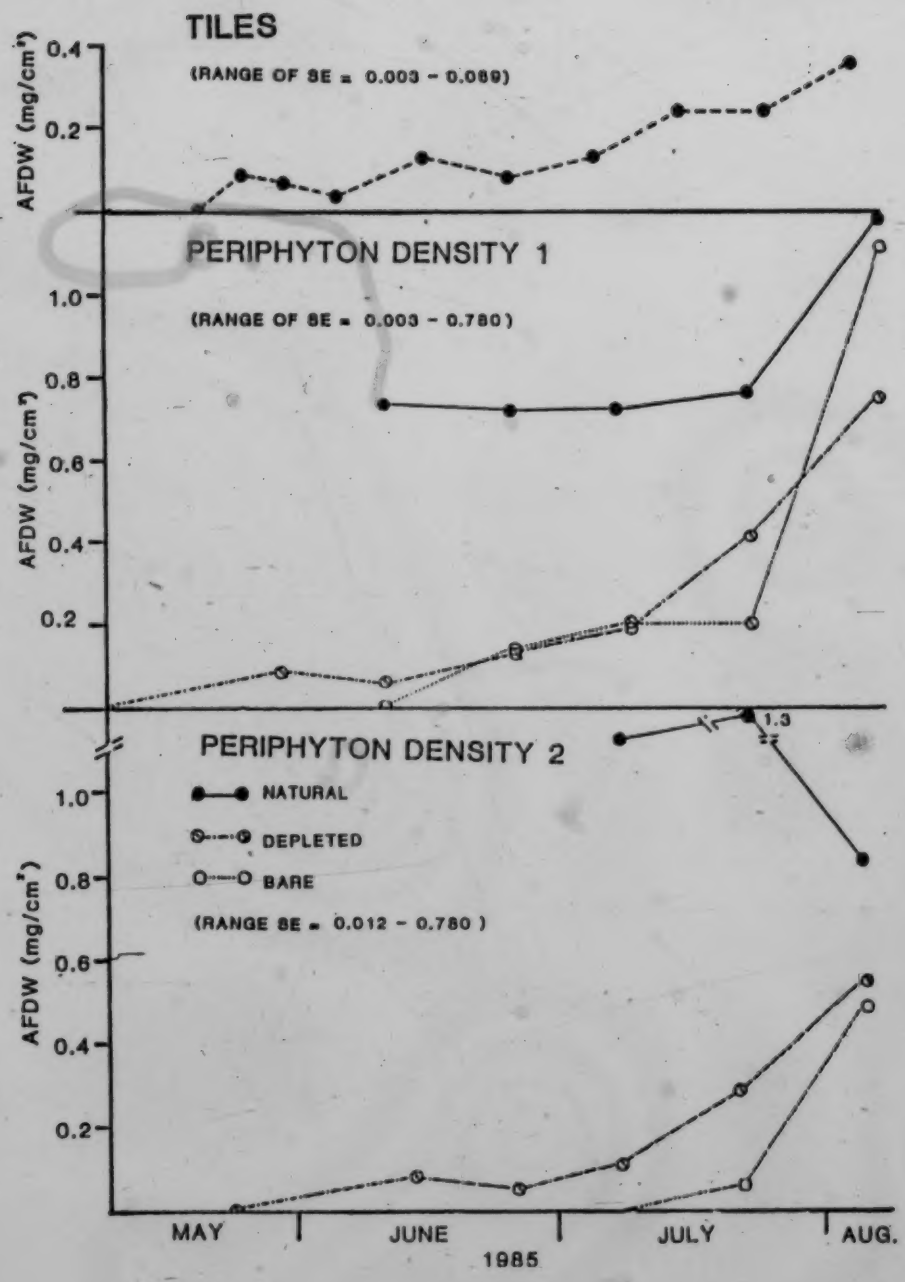


Figure III-5. Accumulation of periphyton (AFDW) on rocks in Periphyton Density 1 and 2 and on tiles. AFDW was quantified on rocks sampled from the natural, depleted and bare treatments during PD1 and PD2 and from depleted treatment rocks before the experiments. Sample sizes for PD1 and PD2 are two rocks from each treatment on each sampling date. Sample sizes for tiles are three tiles on each sampling date.

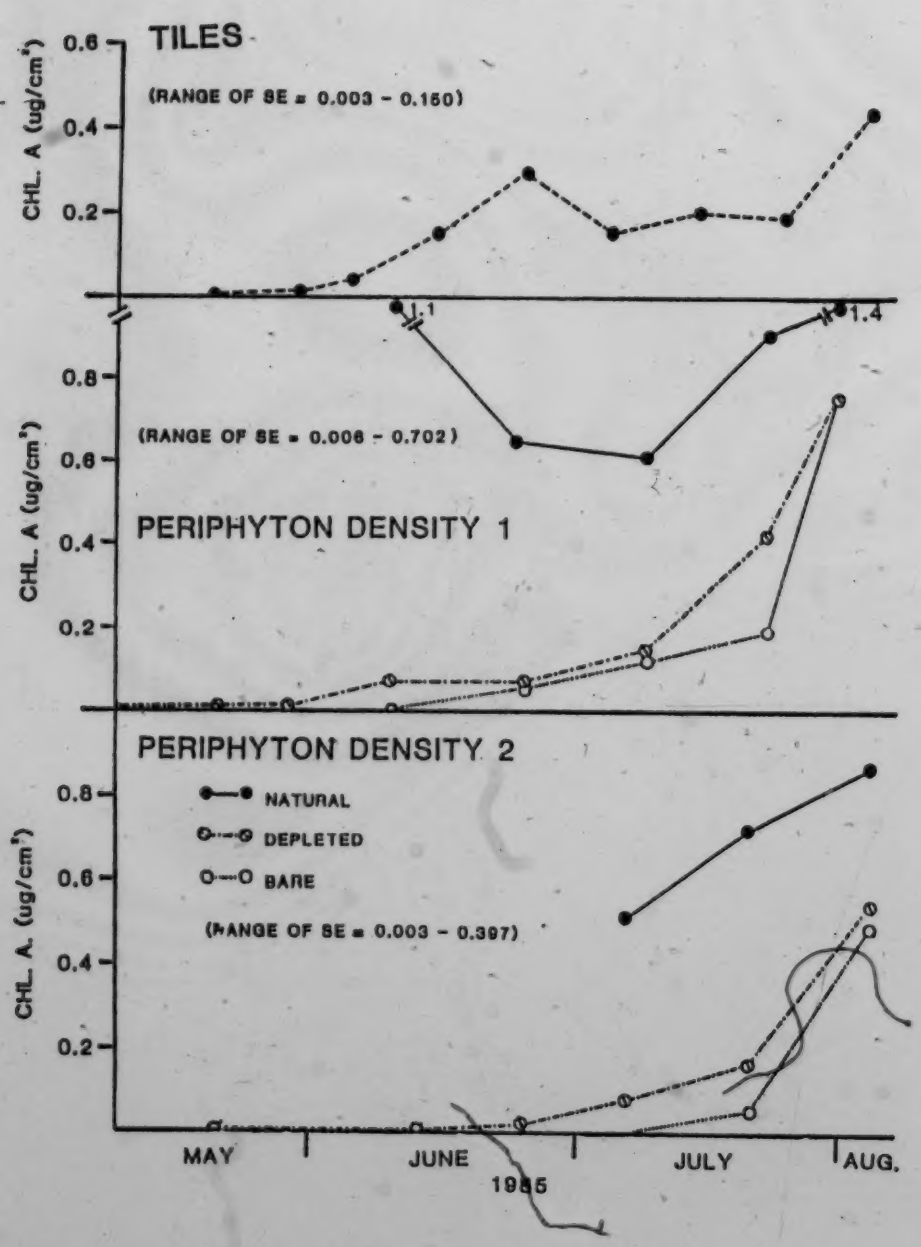


Figure III-6. Accumulation of living algae (chlorophyll a) on rocks in Periphyton Density 1 and 2 and on tiles. Chlorophyll *a* was quantified on rocks sampled from the bare, depleted and natural treatments during PD1 and PD2 and from the depleted treatments before the experiments. Sample sizes for PD1 and PD2 are two rocks for each treatment on each sampling date. Sample sizes for tiles are three on each date.

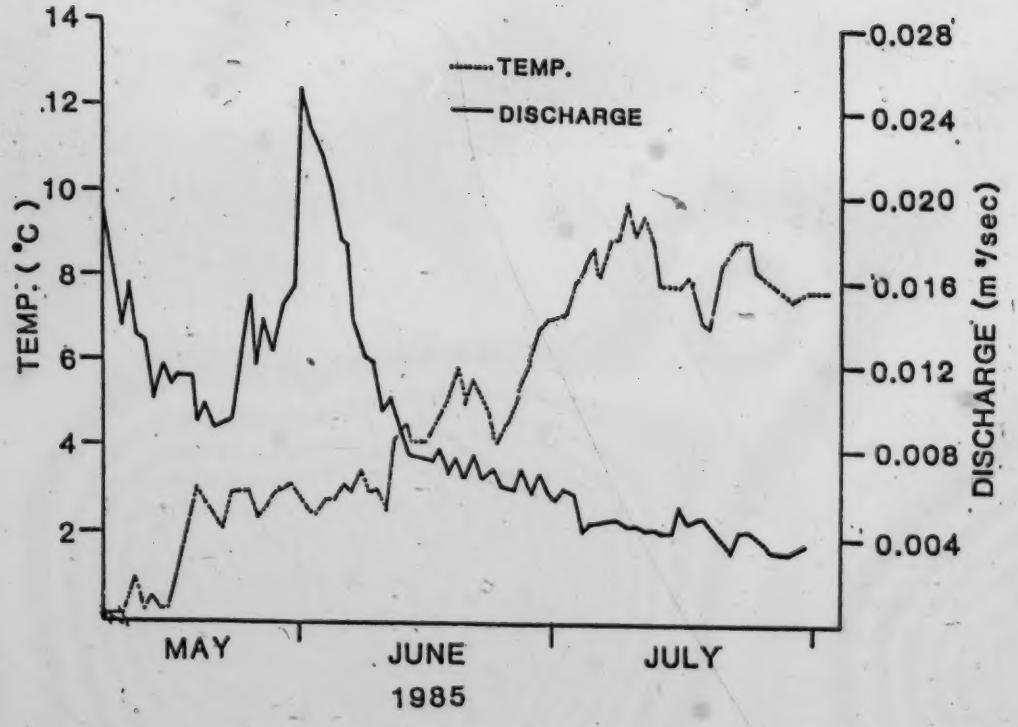


Figure III-7. Temperature and discharge data for Dead Horse Creek, Alberta, May-July, 1985. Recordings were taken at 9.00 am daily.

AFDW (Fig. III-5) on rocks sampled from the bare and depleted treatments. At this time, periphyton had been accumulating on bare rocks for only 14 days but had been accumulating on depleted rocks for 46 days in PD1 and for 58 days in PD2. The difference in periphyton accumulation rates could be caused by the increasing water temperatures and decreasing discharge in Dead Horse Creek over the summer (Fig. III-7). Higher water temperatures probably increase periphyton productivity (Patrick 1977) and lower water flows increase the rate of organic matter sedimentation from the water column (Stevensson 1984). At the completion of both experiments, the densities of periphyton on rocks that had been scraped previously (bare and depleted periphyton treatments) were similar and approximately half the densities measured for natural rocks. These results should be viewed cautiously because mean values were calculated for only two rocks from each treatment. There were large variations in chlorophyll *a* and AFDW densities between rocks within a treatment. To quantify this variation I analysed the periphyton from all rocks scraped to create the bare and depleted treatments. The standard errors for chlorophyll *a* analyses were between 30-41% of the mean and for AFDW analyses between 23-30% of the mean (N=10 or 16). Mean values calculated from two rocks selected randomly from each treatment give only an approximate indication of the periphyton on rocks remaining in the riffle.

The accumulation of periphyton on tiles was very slow. After 75 days the mean chlorophyll *a* and AFDW values for the three tiles sampled were only 0.42 $\mu g/cm^2$ and 0.36 $mg/cm^2$ respectively (Fig.III-5 and III-6) This is less than half the average densities of chlorophyll *a* and AFDW on rock surfaces in Dead Horse Creek riffles (chlorophyll *a* = 1.07 $\mu g/cm^2$, AFDW = 1.20 $mg/cm^2$). This slow rate of periphyton accumulation is probably caused by low water temperatures in Dead Horse Creek. Lamberti and Resh (1983), using similar tiles in a Californian stream, found chlorophyll *a* had reached densities of 0.8 $\mu g/cm^2$ on the bare tiles after only 14 days.

All the periphyton samples were dominated by heterotrophic components of periphyton. The Autotrophic Index or AI is a ratio of AFDW to chlorophyll *a* biomass and

is used to assess the hetero:autotrophic nature of periphyton. Weitzel (1979) suggested that AI values greater than 100 reflect heterotrophic conditions. The mean AI for periphyton from rocks not previously scraped (natural treatment) in PD1 and PD2 was 1024 (SD=528, N=16). Periphyton from the bare and depleted treatment rocks, had an even higher mean AI value. Heterotrophic components of periphyton e.g. FPOM, bacteria, and fungi, may colonize a bare (scraped) surface before colonization by algae. The AI values for tile periphyton samples support this premise because mean AI decreased the longer the bare tiles had been in the stream. Over the first 2 weeks, the mean AI value was 5276 (SD=2989, N=14)), and for the next 4 weeks was 840 (SD=375, N=8).

I was not able to identify or separate the heterotrophic components that constitute the bulk of periphyton biomass in Dead Horse Creek. Dominant autotrophs were the green filamentous algae *Rhizochlonium* sp. and *Chaetophora* sp., and the blue-green algae *Lyngbya* sp. and *Nostoc* sp. Several genera of diatoms including *Cocconeis, Navicula* and *Meridion* were also common in the periphyton samples.

## DISCUSSION

If the 'fitness' of an individual is determined by its net rates of energy gain, behaviours will evolve that maximize these gains within evolutionary and physiological constraints. An ability to locate or remain for longer periods on rocks with higher periphyton densities will increase a grazer's net energetic gains from feeding when periphyton densities vary between rocks. In Dead Horse Creek, periphyton densities vary between rocks, and the dominant grazers *O. zelti, N. alicia* and *Epeorus* are all generalist feeders (see Chapter II). When periphyton densities were experimentally manipulated between rocks, more *O. zelti* larvae occurred on rocks with natural periphyton densites than rocks with lower (depleted and bare treatments) periphyton densities. This result supports the hypothesis that periphyton densities influence the micro-distribution of *O. zelti* larvae between rocks. It also agrees with the finding that *O. zelti* larvae densites are positively correlated with periphyton densities on

individual rocks in Dead Horse Creek.

*Oligophlebodes* larvae may selectively colonize or stay longer on rocks with more periphyton. Charnov (1976) and Pyke (1978) developed models that describe an animal's allocation of time and movement patterns between and within food patches respectively. These models would predict *O. zelti* larvae will spend longer periods on rocks with more periphyton. Studies that track movements of individual larvae are needed to determine the behaviourial mechanism that results in the positive association between densities of *O. zelti* larvae and periphyton on rocks in Dead Horse Creek. It would also be interesting to investigate the methods of sensory perception larvae use to assess periphyton densities, pathways between this sensory perception and movement patterns, and 'decisions' larvae make to stay on or leave a rock.

There were no differences in the abundance of *N. alicia* larvae on rocks with different periphyton densities. This suggests factors other than periphyton density influenced the micro-distribution of *N. alicia* between rocks. Many abiotic variables, e.g. water velocity (Minshall and Minshall 1977) and substrate composition (Culp *et al.* 1983, Erman and Erman 1984)) and biotic variables, e.g. competition (McAuliffe 1984) and predation ( Peckarsky and Dodson 1980, Flecker 1984) have been shown to influence the micro-distribution of freshwater benthic invertebrates. The colonization of rocks by *N. alicia* larvae may be influenced by water velocities in Dead Horse Creek. *Neothremma alicia* larvae occur in riffles with higher mean water velocities and lower periphyton densities than riffles dominated by *O. zelti* larvae (see Chapter II). *Neothremma* larvae seem morphologically suited to high water velocities; the larval case is extremely slender and covered externally with a thin layer of silk.

Abundances of *Epeorus* sp. nymphs were highest on depleted periphyton rocks in both periphyton density experiments. The body of *Epeorus* nymphs is dorso-ventrally flattened with wide femora extending laterally from the thorax. I suspect the ventral surface of nymphs are very close to the rock surface as they move across rocks. Rocks with less periphyton (depleted and bare treatments) must have had smoother surfaces than natural

rocks and could have been preferentially colonized by *Epeorus* sp. nymphs for this reason. Despite this preference for smoother surfaces, *Epeorus* nymphs did not colonize bare rocks until the rocks had been in the riffle 10-13 days, which indicates the nymphs can detect and avoid rocks with little periphyton.

The size of periphyton food patches within an artificial tile (over the range tested) did not influence the colonization of tiles by *N. alicia* larvae in Dead Horse Creek. Equal numbers of *N. alicia* larvae occurred on tiles that were covered with periphyton, tiles that were half covered with periphyton and tiles that were two quarters covered in periphyton. It appears that *N. alicia* larvae will colonize a substrate regardless of the size of periphyton patches or the density of periphyton on that substrate. However, on a smaller spatial scale (within a substrate), the micro-distribution of *N. alicia* larvae may be influenced by distributions of periphyton densities. *Neothremma* larvae were found almost exclusively on periphyton patches and not bare areas on the tile surfaces. Kohler (1984) found that movement rates for *Baetis tricaudatus* nymphs were significantly greater between periphyton patches than within patches on a tile. *Neothremma* larvae could be exhibiting a similar behaviour on rocks in Dead Horse Creek riffles.

The patchy distribution of periphyton densities (created in these experiments) influenced the micro-distribution of all three taxa studied. *Oligophlebodes* larvae and *Epeorus* nymphs appeared to preferentially colonize rocks with natural periphyton and depleted periphyton densities respectively. Abundances of *N. alicia* larvae did not vary between rocks with different periphyton densities, but on individual tiles *N. alicia* larvae were found on periphyton patches and not bare areas. I can only speculate whether the foraging behaviours that result in these micro-distributions have evolved to maximize grazer's net rates of energy gain. The wide range of periphyton densities between rocks and the non-selective diets of *O. zelti* larvae support the premise that net rates of energy gain will be maximized for an *O. zelti* larva when it feeds on a rock with high periphyton densities. The preference for rocks with depleted periphyton densities by *Epeorus* nymphs may maximize net rates of energy gain if

nymphs expend less energy moving across smoother surfaces. Alternatively, on this spatial scale (between rocks), the distribution of *Epeorus* nymphs may be primarily influenced by another environmental variable. This does not rule out the possibility that *Epeorus* respond to patchy periphyton densities on a larger spatial scale. For example, *Epeorus* nymphs may occur in areas of riffles that have higher periphyton densities.

The importance of scale is exemplified by the different responses of *N. alicia* larvae to patchy periphyton densities at different spatial scales. Micro-distribution of *N. alicia* larvae between rocks may be influenced primarily by water velocities, but within a substrate *N. alicia* micro-distributions appear to be influenced by periphyton densities. Periphyton could influence the distributions of grazers on a range of spatial scales. For example, Wiggins and Mackay (1978) suggest periphyton and grazer distribution are related across North America and Kohler (1984) showed periphyton densities affect grazer micro-distributions on tile surfaces. Studies that investigate the association between distributions of periphyton and a grazer species on different spatial scales are needed before we can assess the extent periphyton influences grazer distributions in streams.

Periphyton will be a limiting resource when the amounts required by grazers for maximizing energy gains (within environmental and physiological constraints) are greater than the amounts available. In Dead Horse Creek, it is very unlikely that periphyton is limiting because grazing caddis larvae probably consume less than 1% of the periphyton on an average rock per day (Chapter II). Most lotic grazer-periphyton studies have been done in streams where periphyton is limiting. McAuliffe (1984) showed *Glossosoma* (Trichoptera:Glossosomatidae) larvae competed for a limited periphyton resource, and Hart (1981) suggested that movement patterns of *Dicoesmoecus gilvipes* (Trichoptera:Limnephilidae) larvae were a response to limited periphyton. In streams where the ratio of periphyton : grazer densities are very low, grazers will significantly deplete the standing crop of periphyton (Lamberti and Resh 1983, Eichenberger and Schlatter 1978). In Dead Horse Creek, there is probably an overabundance of periphyton on an average rock, and

it is the range of periphyton densities between rocks and within rocks that influences the micro-distribution of *O. zelti*, *N. alicia*, and *Epeorus*. My study demonstrates that patchy periphyton distributions, on different spatial scales, can influence the micro-distributions of grazing macroinvertebrates.

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# IV. GENERAL DISCUSSION

## Feeding

Because benthic invertebrates are mainly generalist (non selective) feeders and have diets that vary with season, life cycle stage and locality, Cummins (1973) suggested feeding group divisions should be based on food acquiring mechanisms, not food consumed. He divided benthic invertebrates into four functional feeding groups : shredders, collectors (including filter feeders and deposit feeders), scrapers (or grazers) and predators. From the analysis of *O. zelti* and *N. alicia* larvae's gut contents and mouthparts, I conclude that both species are generalist grazers. The larvae probably ingest any particles within the periphyton that are smaller than the width of larval mouth openings (125 um). Hence gut contents are mainly fine particulate organic matter (FPOM) and diatoms. Previous studies also report grazer gut contents consisted mainly of FPOM, with seasonally variable percentages of diatoms (e.g. Gray and Ward 1979, Hamilton and Clifford 1983, Short 1983, Hawkins 1985). The lack of food selection by grazers in streams may, in part, be caused by the structure of periphyton on rock surfaces. Components of periphyton (fungi, algae, bacteria, organic and inorganic particles) are bound within a mesh of polysaccharide filaments or slime (Lock 1983). *Oligophlebodes zelti* and *N. alicia* larvae have scoop-shaped mandibles and it seems unlikely they could select a particular food item that is enmeshed in these filaments.

The diets of grazing macroinvertebrates and the components of the periphyton must both be assessed before we can quantify grazer-periphyton interactions in streams. Studies investigating the influence of grazers on periphyton densities have often used chlorophyll *a* analyses to quantify periphyton (Lamberti and Resh 1983, Jacoby 1985). If filamentous algae is common on rock surfaces but not ingested by grazers because the algae is too large, chlorophyll *a* will be an erroneous measurement of the grazer's food source. In Dead Horse Creek, periphyton samples were mainly heterotrophic; living algae only constituted an average of 6% of the periphyton biomass. Heterotrophic FPOM dominated the gut contents of all

grazing animals that were dissected. If grazer diets and the periphyton on rocks are mainly heterotrophic (which may be the case in other shady streams), total periphyton biomass (AFDW) and not chlorophyll *a* analyses should be used to investigate grazer-periphyton interactions.

The heterotrophic component of periphyton is a mixture of humic substances, formed as a result of microbial activity on plant and animal material (Wetzel 1975), fungi, bacteria and polysaccharide filaments. Dissolved organic carbon (DOC) is incorporated into the periphyton by precipitation, complexing, flocculation and abiotic absorption (Rounick and Winterbourn 1983). It is not known whether most heterotrophic organic matter originates from autochthonous or allochthonous sources. Rounick *et al.* (1982) used stable carbon isotope analysis to show that faunas of small forested streams utilized mainly allochthonous carbon sources. Dead Horse Creek is shaded by a thick spruce and aspen canopy and the energy base for grazing invertebrates probably originates from allochthonous sources. Techniques that separate the autochthonous and allochthonous portions of periphyton and determine the energy contribution of each to benthic invertebrates are needed before the nature of the energy base for stream communities is completely understood.

**Micro-distribution**

Wiggins and Mackay (1978) suggest grazing caddis larvae in North America are more abundant in western than eastern mountain streams, because western streams receive more sunlight and probably support more diatoms. Similarly, the River Continuum Concept (Vannote *et al.* 1980) predicts that grazers will dominate in the open downstream stretches of a lotic system. However, the premise that sunlight increases autotrophic production and in turn supports greater grazer populations might be too simplistic to explain the distribution of grazers in streams. Dead Horse Creek is highly shaded but supports large populations of grazers. All grazing taxa in Dead Horse Creek fed mainly on the FPOM component of the periphyton, which is mainly heterotrophic and hence not influenced by sunlight. Highest

overall densities of grazers (e.g *O. zelti* and *Epeorus* sp.) and periphyton occurred in the mid-section of the study area. These sections had lower slopes and water velocities than the upstream and downstream stretches. Statzner and Higler (1986) suggested slopes and the resulting water flow characteristics govern the zonation of benthos along a stream. Since lower water velocities increase sedimentation rates of organic matter from the water column (Stevensson 1984), both higher periphyton and grazer densities in the mid-section of the study area may be attributable to riffle slopes instead of sunlight.

A close relationship between the distributions of grazers and periphyton in streams has been previously observed, but only in streams with much higher grazer and lower periphyton densities than Dead Horse Creek (e.g. Lamberti and Resh 1983, McAuliffe 1984). If grazers are competing for periphyton, natural selection will favour individuals that locate and remain on rocks with greater periphyton densities. On an average rock in Dead Horse Creek, there appears to be 100X more periphyton than the caddis larvae on the rock could consume. This is probably an overestimate because some periphyton may be bound (by polysaccharide filaments) into particles that are too large for a caddis larvae to consume. Despite this, it seems unlikely periphyton is a limiting food resource in Dead Horse Creek.

I conclude that the variable (patchily distributed) periphyton densities between rocks in Dead Horse Creek riffles is responsible for the evolution of foraging behaviours that enable *O. zelti* larvae to locate or remain for longer periods on rocks with more periphyton. The generalist non-selective diets of *O. zelti* support the idea that these foraging behaviours maximize energy gains for the larvae. However, the conclusion is still dependent on the assumption that natural selection has favoured animals that maximize rates of energy gain. This assumption forms the basis of optimal foraging models. Hence, the agreement between observed foraging behaviours and those predicted by the models, for a wide range of aquatic and terrestrial animals, argues for the validity of the assumption. (see reviews in Pyke *et al.* 1977, Townsend and Hughes 1981). Foraging behaviour is only one way an animal can increase its energetic gains. An animal may evolve physiological strategies such as increasing

assimilation efficiencies to increase energetic gains. These strategies and the evidence for their evolution (e.g. the positive correlation between fecundity and size) are reviewed by Calow (1977).

*Neothremma* larvae occur in riffles upstream and downstream of riffles dominated by *O. zelti* larvae in Dead Horse Creek. The *N. alicia* dominated riffles in Dead Horse Creek had higher water velocities and lower periphyton densities. *Neothremma* appears suited to this microhabitat because the larval case is streamlined and larvae have slower growth rates than *O. zelti* larvae. Periphyton densities do not appear to influence the micro-distribution of *N. alicia* between rocks. *Neothremma* and periphyton densities were not correlated on rocks and the larvae did not preferentially colonize rocks with more periphyton. However, *N. alicia* larvae do locate or spend longer periods on patches of periphyton within a substrate.

The position of an animal at any point in time must be influenced by the interactions of many environmental variables on different spatial scales. Knowledge of the life histories, and the factors that influence distributions of benthic macroinvertebrates on different spatial scales, will eventually lead to a better understanding of the function and structure of aquatic communities.

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